Impact of competition on the early growth and physiological responses of *potential short-rotation forestry species in Ireland*

PhD thesis

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Abstract

To develop best practice for managing short rotation forestry (SRF) systems in Ireland more information about how planting density can be used to maximise productive potential is required. To this end, the morphological and physiological responses to various planting densities were investigated for three potential SRF species. A field trial and a polytunnel experiment were established to examine the effects of various planting densities on the growth of shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière). In the polytunnel experiment, trees were planted at densities of 1, 4 and 8 plants per pot and observed over a period of less than 1 year. Four planting densities ranging from 1,333 to 40,000 stems ha^{-1} were used in the field trial and measurements were carried out over a 4-year period. Crown area and leaf chlorophyll concentration (Ch_{leaf}) declined significantly as planting density increased in *E. nitens* but photosynthesis rates (P_N) were unaffected. This resulted in a small but very productive crown in *E. nitens*. As planting density increased, *A. cordata* trees became significantly taller with thinner stems and a wide-reaching crown but maintained a similar leaf size and Ch_{leaf}. However, P_N rate declined with planting density in *A. cordata*. Height, stem diameter and branch length declined as density increased in *P. sitchensis*, but there was very little response to competition in the field trial, apart from at the leaf level. More biomass was allocated to below-ground than above-ground components at all planting densities in *P. sitchensis* while also producing a very dense crown. The quantities of above-ground biomass produced by year four were similar in *A. cordata* and *P. sitchensis,* whereas *E. nitens* produced the greatest quantity of biomass of the species examined in the field trial. Projections of future growth and biomass yield were made using a process-based model (3-PG). This approach also allowed a consideration of the planting density and rotation length most likely to suit each species. A standard SRF rotation length of 15 years was used during modelling to compare the productivity of the three species established at various planting densities. The optimum planting density and biomass yield[1] predicted for each species were: 3,900 - 4,500 stems ha^{-1} with c. 150 t ha^{-1} for *E. nitens*; 15,600 – 20,400

[1] Above-ground woody biomass (AWB).

stems ha^{-1} with c. 52 t ha^{-1} for *A. cordata*; 1,600 – 2,500 stems ha^{-1} with 85 t ha^{-1} for *P. sitchensis*. The rapid growth rate and high biomass yield over a short rotation indicate that *E. nitens* is a suitable species for SRF. However, the other two species would appear not to be suited to management in such a system. The rapid growth of *A. cordata* produced slender stems and long branches which enabled it to compete at high planting densities, but it did not produce the biomass yield that is required for SRF. Although *P. sitchensis* produced a very dense crown with a high wood density at high stocking, this did not compensate for the low biomass yield of this species, making it a less attractive choice for SRF systems.

Statement of original authorship

I hereby certify that the submitted work is my work, was completed while registered as a candidate for the degree stated on the title page, and I have not obtained a degree elsewhere on the basis of the research presented in this submitted work.

Susan Foreman

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Abbreviations and Acronyms

Above-ground woody biomass	AWB
Acidity scale	pH
Alnus cordata (Italian alder)	IA
Analysis of variance	ANOVA
Below ground biomass	BGB
Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie	BBCH
Branch length	BL
Confidence limit	CL
Constant in stem mass v. diameter relationship	α_S
Copper	Cu
County	Co.
Crown depth	CD
Crown height	CH
Current annual increment	CAI
Denmark	DK
Density of water	ρwater
Department of Agriculture, Food and the Marine	DAFM
Diameter at breast height	DBH
Dry weight	DW
Estimation and statistical inference for generalized linear mixed models	glimmix
Eucalyptus nitens	EN
Foliage: stem partitioning ration @ 2 cm	pFS_2
Foliage: stem partitioning ration @ 20 cm	pFS_{20}
Generalised linear mixed models	GLM
Green volume	GV
Hectare	Ha
Improved Washington	IW
Leaf	L
Leaf area	LA
Leaf area index	LAI
Leaf chlorophyll content	Ch_{leaf}
Leaf plastochron index	LPI
Light emitting diode	LED
Magnesium	Mg
Manganese	Mn
Mean annual increment	MAI
Megajoule per metre squared	MJ m^{-2}
Micromole	µmol
Net primary production	NPP
New Zealand	NZ
Nitrogen	N
Oven dry mass	ODM
Percentage dry weight	% dw

Phosphorus	P
Photosynthetic active radiation	PAR
Picea sitchensis (Sitka spruce)	SS
Plastochron index	PI
Potassium	K
Power in stem mass v. diameter relationship	n_S
Projected crown area	PCA
Red: far red ratio	R: FR
Representative concentration pathways	RCP
Root biomass	RB
Root collar diameter	RCD
Saturated vapour pressure	*SatVapPres*
Species	Spp
Specific gravity	SG
Specific leaf area	SLA
Stand volume	SV
Standard error	SE
Statistical Analysis System	SAS
Temperature maximum	Tmax
Temperature minimum	Tmin
United Kingdom	UK
United States of America	USA
Vapour pressure deficit	VPD
Zinc	Zn

1 Introduction

The United Nations Framework Convention on Climate Change is an international environmental treaty whose main aim is to limit the impact of climate change. The Kyoto Protocol extends the convention treaty by imposing binding greenhouse-gas emissions reduction targets on its signatories. As a signatory of the treaty and member of the European Union, Ireland has commitments to comply with the Kyoto Protocol through an EU directive. In addition, the renewable Energy Directive (EU Directive 2009/28 EC) mandates the use of energy from renewable sources. The members of the EU agreed an overall 20% increase in energy efficiency, a 20% reduction in greenhouse gas emissions, and an increase to 20% energy generation from renewable resources by 2020 (European Union, 2009). Ireland is required to achieve 16% of energy usage from renewable resources by 2020. In 2018 the Renewable Energy Directive was revised (Directive 2018/2001/EU) and aims to maintain the EU as a global leader in the use of energy generation from renewable resources. The updated directive establishes new and binding overall renewable energy targets for the EU of at least 32% for 2030.

The directive requires that member states increase the utilisation of existing timber resources and stimulate new and innovative approaches to generate new resources, such as short rotation forestry (SRF) or biofuel from municipal or agricultural waste (European Union, 2009). All EU member states are required to establish a national renewable energy action plan (NREAP) with targets for biomass use. The 2009 NREAP report sets Ireland's national targets for the period 2009 – 2020 and includes policies to develop new biomass resources. Biomass includes solid, biogas and bioliquids. This report estimated that in 2006 there were only 63 ha of SRF in Ireland which were managed specifically to produce an energy crop. NREAP 2010 committed Ireland to producing c. 700 GWh of energy generated annually from solid biomass by 2020 (DOCCAE, 2010).

Sources of biomass can include residues from forestry, sawmills, wood industry by-products (e.g. bark), recycled post-consumer products and pulpwood and purpose-grown biomass, including SRF and short rotation coppice (SRC) to supply the energy industry. In 2010, the wood panelling and sawmills sectors were the main users of

biomass, using it as a feedstock for heat generation in processing and drying kilns (Knaggs and O'Driscoll, 2012). However, the biggest users of biomass in Ireland in the future will likely be the three main electricity-generating power stations. In the past, these stations burned peat, but co-firing with biomass began at the Edenderry station in 2008. In 2016, 1.58 million m^3 of wood energy was consumed in Ireland to generate energy (Phillips et al., 2016). It is estimated that by 2020 the demand for wood to meet the national energy demand will have risen to approximately double that figure. This will result in a deficit of 1.4 million m^3 in Ireland (Wood Mobilisation and Production Forecasting Group, 2018). To meet the rising demand, more biomass crops will have to be grown in Ireland.

The latest National Forest Inventory report estimated that forest cover in Ireland has reached 11% (770,000 ha) (DAFM, 2017). Forests in Ireland are predominantly managed using a clear fell cut-to-length system servicing a buoyant timber industry supplying raw material mainly to pulp mills and sawmills. The timber industry currently cannot bridge the deficit in supply of raw material, so dedicated energy crops must be grown to help meet the shortfall. Although SRF afforestation grants are available from the Department of Agriculture, Food and the Marine (DAFM) to encourage growers to supply the requirements of the renewable energy sector, there has been very little uptake of the scheme by private landowners. It is likely that one of the reasons for the low uptake has been a lack of knowledge among forest managers, practitioners and landowners about the most suitable species and best establishment and management practices specific to SRF systems under Irish conditions. Species recommended for use in SRF in Ireland under the Forestry for Fibre scheme by DAFM are *Alnus cordata*, *Eucalyptus glaucescens, E. gunnii, E. nitens, E. rodwayi and E. subcrenulata, Populus tremula* x *tremuloides* and a selection of seven *Populus* clones (DAFM, 2018). However, there is limited experience in growing energy crops in Ireland. Short rotation coppice has received some attention, but not much research has been dedicated to the issue of SRF worldwide in general, and in Ireland in particular.

Short rotation forestry systems aim to produce large quantities of dry matter per unit area within a short rotation. One of the main factors affecting productivity,

particularly over short rotations, and which can be manipulated directly through management, is planting density. Planting density influences initial costs, rotation length, wood quality and final yield (Benomar et al., 2012). Much is known about stocking density and its impact on height, stem diameter and final yield in long-rotation conventional forestry systems. However, comparatively little is known about the initial competition interactions between trees, especially early in the rotation.

Climatic conditions, stress levels etc., affect a plant's physiological functioning, including the photosynthetic processes. Higher planting densities will intensify competition between the individual tree crowns, increasing the density of the overall canopy which may be manifested in the physiological responses. A plant will alter leaf area and light harvesting capacity, affecting the photosynthetic capacity of the crown as a whole (Niinemets, 2016). Sun and shade leaves tend to have different responses to light availability in response to different planting densities (Michael et al., 1990). Shade leaves often contain more chlorophyll than sun leaves (Taiz and Zeiger, 2010). Therefore, information on physiological responses may help explain differences in productivity between species in response to planting density.

Forest stands respond to climatic and environmental conditions over a long period of time. Many different management approaches (e.g. initial spacing, and silvicultural treatments) may affect productivity potential. Modelling enables forest researchers to relate silvicultural knowledge with ecological information and convert research outcomes into practical expertise (Bartelink and Mohren, 2004). A range of scenarios and their likely impact on growth, rotation and yield can be predicted using models. In this study, modelling was used to assess the likely impact of spacing and silvicultural treatments on early growth characteristics. Furthermore, a modelling approach allows an investigation into the impact of anticipated climate changes on SRF systems in Ireland. Maximising productivity sustainably will depend on the use of suitable silvicultural management system, including optimising planting density to suit each species. A model that can accurately predict the impact on productivity of changes in silvicultural management would be a useful tool in SRF research and practice.

The ShortFor research project was funded from 2014 to 2018 and involved collaboration between University College Dublin, Trinity College Dublin, University College Limerick, Teagasc, Waterford Institute of Technology and Coillte. The project aimed to evaluate silvicultural practices using field trials and other approaches to investigate the potential of SRF systems for biomass production in Ireland. As part of the ShortFor project, the growth dynamics of shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) in response to different planting densities and their likely suitability for biomass production over short rotations were investigated. The main aim of this research was to investigate how competition, arising from increasing planting density, may affect morphological and physiological responses as well as the productivity potential of those species managed in a SRF system. In comparison with other plant research, determining growth response in tree species takes a relatively long time. To this end, a field trial was established as part of the research project, complemented by an experimental study carried out in a polytunnel, to examine planting density effects up to four years after planting. A process-based model was used to estimate future growth and rotation lengths, utilising the data obtained in the polytunnel and field trial. The objectives of the study were to:

- identify the morphological and physiological growth characteristics most affected by competition during an early development period (up to 4 years);
- determine the planting densities which are likely to result in a high biomass yield;
- predict a range of rotation lengths and yields using a modelling approach.

2 Literature review

Short-rotation forestry (SRF) systems are a relatively new method of management in Ireland. Species recommended for use in SRF in Ireland under the Forestry for Fibre scheme by the Department of Agriculture, Food and the Marine (DAFM) are *Alnus cordata*, *E. glaucescens, E. gunnii, E. nitens, E. rodwayi and E. subcrenulata, Populus tremula* x *tremuloides* and a selection of seven *Populus* clones (DAFM, 2018). Several tree species have been suggested as suitable for SRF in the UK, based on their fast early-stage growth rates: e.g. *Fraxinus excelsior, Acer pseudoplatanus, Betula pendula, P. tremula* x *tremuloides. Nothofagus alpina* syn*. N. procera, Alnus cordata, A. rubra*, *Eucalyptus nitens, E. gunnii* and *E. glaucescens* (McKay, 2011). However, to increase productivity per unit area, stocking density may be increased and rotation length reduced (McCarthy, 1979). However, such changes to conventional systems result in higher levels of competition at an earlier stage, which may affect the morphological and physiological responses of trees, as well as biomass production and the proportional amounts allocated to different tree parts. This review will focus on three potential SRF species for production in Ireland, specifically *E. nitens, A. cordata* and *P. sitchensis.* The potential of these species in SRF has been discussed in more detail below.

2.1 A case for short-rotation forestry

EU Directive 2009/28 EC promotes the use of energy from renewable sources with a view to achieving the goals set at the Kyoto Convention. The directive requires Ireland to obtain 16% of its energy from renewable resources by 2020 (European Union, 2009). Biomass production from short-rotation forestry might assist Ireland in meeting this target. However, there is little information available on the criteria for choosing suitable species, nor on best practice for managing SRF systems in Ireland, especially in relation to optimum planting densities and rotation lengths.

Several forestry systems are used in Ireland, the most widely employed being conventional thinning-based systems, short rotation forestry (SRF) and short rotation coppice (SRC) are also used but far less commonly. Management and establishment of conventional coniferous plantations, although species dependent, are generally based on an initial stocking density of 2,500 stems ha^{-1}. Fast growing species such as

P. sitchensis can be clear felled in rotations of c. 30 years. Short-rotation coppice is in general a densely-planted high-yielding crop, harvested every 2-3 years depending on the species. Short-rotation forestry systems are defined as the silvicultural practice of managing fast-growing tree species to produce biomass within 8-20 years (McKay, 2011; Parsons, 2006). The rotation length for SRF systems is intermediate between conventional forestry (30-80 years at c. 2,500 stems ha^{-1}) and coppice systems (2-5 years at c. 15,600 stem ha^{-1}). In a review of SRF and its environmental impacts, McKay (2011) found the quality and quantity of existing growth data inadequate in the UK for generating accurate predictions of yield for SRF systems and to support and advance the development of SRF. The rotation lengths and planting densities recommended for SRF have been based mostly on experience from conventional practices rather than on data derived from field trials (McKay, 2011). There is little information about the potential of SRF systems, the choice of suitable species and the specific requirements for management, e.g. planting densities, rotation lengths and silviculture (Kerr, 2011; McKay, 2011).

Management of any forestry system depends on the type of product being produced. An important consideration in the quality of biomass for energy, is the proportion of wood to bark (Kauter et al., 2003). Conventional forestry results in the production of large-dimension saw-log over a long rotation; SRC produces a biomass energy crop, but the material is small dimensioned, grown with multiple stems, and as it is produced in a short period, results in the production of wood that has a low wood to bark ratio. SRF concentrates on the production of single-stemmed trees, similar to conventional forestry. However, the trees must grow rapidly, exploiting site resources quickly resulting in the production of material with a higher wood to bark ratio over a longer rotation than for SRC (Kauter et al., 2003). The biomass from SRF systems is likely to be used in boilers for power production and as such the characteristics of calorific value, chemical composition, wood density, moisture and ash content are all important. Species selected for SRF systems ideally need to combine a high basic wood density with a rapid growth rate and be suited to high productivity over a short rotation period (Neilan and Thompson, 2008).

Biomass is generally regarded as a rapidly renewable organic product resulting from the process of photosynthesis. It comprises the biodegradable product or waste material from the agriculture, aquaculture or forestry industries, and its yield is usually expressed as oven-dry tons per unit area (Brown, 1997). Producing the greatest biomass yield in a relatively short timeframe is an important strategy in energy production from renewable and carbon-neutral sources. Much research has been carried out internationally in the area of SRC, which has identified species such as *Salix* and *Populus* for use under SRC. These species are often favoured for their high growth rates over short rotations. However, the material produced is not always ideal as fuel wood. Ramsay (2004) suggests an ideal fuel should have a) low moisture content b) high wood density, c) possess suitable chemical characteristics (i.e. low in chloride and sulphur), and d) be easily harvestable.

2.2 Species selection

SRF aims to exploit species with fast juvenile growth rates to produce biomass with a high wood density, before competition for light and nutrients reduces development (MacDonald and Hubert, 2002). To fully exploit and manage the production potential of any species in a short rotation, the factors that influence growth and production need to be understood (Michael et al., 1988). Different species may vary in their response to environmental conditions, thus influencing growth potential (Michael et al., 1990). In general, species selection for conventional forestry use is frequently based on defect elimination, e.g. smaller branching habit, straightness of stem (Dickmann, 1975). However, selection of species suitable for SRF systems should be based on their silvicultural characteristics and suitability to site and climatic conditions, but particularly for their ability to grow rapidly during the juvenile period.

Research elsewhere in Europe during the last four decades into short-rotation biomass production has focused on relatively few species, using mostly SRC with some using SRF (Table 2-1). Owing to their rapid juvenile growth (Bergez et al., 1989), high photosynthetic capacity (Barigah et al., 1994) and rapid woody biomass accumulation (Hansen, 1991), *Populus* hybrids have been the focus of many SRC trials. However, SRF may involve mixed species production to spread the risk and increase the efficiency of conversion of solar radiation to biomass (McKay, 2011).

Few species have been examined for their SRF potential in Ireland (de Miguel Muñoz et al., 2016). Several species of eucalyptus (*E. nitens* (H. Deane & Maiden), *E. gunnii* (Hook.f) and *E. delegatensis* (R.T.Baker) were planted in the last eight years, mostly in the south and east as SRF crops (Coates et al., 2017). Previous to 2003 approximately 80 ha^{-1} of hybrid poplar were planted on a short rotation basis (Keary, 2003).

2.2.1 *E. nitens*

Eucalyptus is part of the Myrtaceae family which comprises around 800 species and is native to Australia, New Guinea and parts of Indonesia (Stevens, 2001). It is one of the most widely-planted hardwoods in tropical areas (Rockwood et al., 2008). According to Campoe et al. (2012), a good understanding of the ecophysiology of growth of eucalyptus species is still lacking. *E. nitens* originates from areas where soil nutrient availability is limited (Thompson et al., 2012). Therefore, although the productivity of *E. nitens* grown in Australia is high, maximum growth rates are rarely achieved in these regions mainly due to nutrient and water limitations (Whitehead and Beadle, 2004).

Eucalyptus growth potential in Ireland was first investigated, with the laying down of field trials in Avondale in 1908 (Neilan and Thompson, 2008). However, there is still a great deal unknown about the growth of eucalyptus under Irish conditions (Thompson et al., 2012). Trials planted before 1992 in Ireland revealed that *E. nitens, E. urnigera* and *E. johnstonii* were the most productive of those evaluated (Neilan and Thompson, 2008). Further trials established in 1992 and 1993 used species selected specifically for their frost hardiness, rapid production potential and stem form, namely *E. nitens, E. delagatensis* and *E. gunnii.* After nine years growth, *E. delagatensis* and *E. gunnii* grew in excess of 1 m height per year, with *E. nitens* growing more than 1.5 m per year, but height growth varied between 1-2 m between sites in all species. The relatively rapid early growth under Irish conditions makes *E. nitens* an ideal candidate for SRF (Thompson et al., 2012).

Growth rates were highly variable across stands in a study of eucalyptus carried out in Brazil, although the plant material, fertilisation, and soil preparation methods and management practices used were similar across sites (Campoe et al., 2012).

Differences in topography, soil texture, water availability and nutrient content may instead explain this variation. However, high variability in growth rate was also observed in a stand of *E. nitens* in Tasmania on a highly uniform site; the high variability was attributed to genetic factors (Neilsen and Gerrand, 1999).

There are several challenges in relation to growing *E. nitens* in Ireland, which include its low level of frost hardiness during the winter and a tendency to blow over (Leslie and Purse, 2016) and high mortality during establishment (Coates et al., 2017). High mortality rates have been reported for *E. nitens* growing in plantations in Ireland. In a recent survey mortality ranged from 11% to 62% with an average of 28% recorded across 15 sites in Ireland (where the trees in 13 sites were between 5-7 years old and the trees on 2 sites were 22-23 years old) (Coates et al., 2017). High mortality rates also have been observed in eucalyptus in other countries. In a study in Tasmania a mortality rate 2 years after planting of 24.9% from unknown causes was reported (Close et al., 2006).

The high mortality rate at establishment may be attributed to the methods employed during handling and planting. Eucalpytus seedlings are generally grown in Ireland from seed and sold with their root system contained in a plug of growing media (Thompson et al., 2012). Seedlings need to initiate new root growth soon after planting to access water and nutrients to ensure successful establishment (Grossnickle, 2005). If contact between the plug medium and soil after planting is poor the seedlings may become susceptible to drought stress (Bernier et al., 1995; Stape et al., 2010). Eucalyptus are also highly sensitive to weed competition (Bennett and Leslie, 2003) and weed control is essential during establishment since the planting stock is normally small and may be outcompeted by weeds (McNabb, 1994; Neilan and Thompson, 2008).

Eucalyptus frost hardiness levels differ with species. Prolonged cold periods will affect even the hardiest eucalypts. In 2008/09, low winter temperatures of -7 °C badly damaged *E. nitens* and all the *E. globulus* were killed in a trial in Ireland (Thompson et al., 2012). Subsequently, sustained low temperatures of -16 °C were recorded in December 2010, which killed all the *E. nitens* seedlings in the same trial (Thompson et al., 2012). Prolonged cold temperatures of -14 °C also severely damaged 11 year-old

E. nitens, which was about 10 m tall, growing in another field trial in Sligo (Neilan and Thompson, 2008). Therefore, it is not surprising that it is recommended that *E. nitens* should only be planted in locations associated with low risk of frost, e.g. sites within 50 km of the coast (DAFM, 2018; Thompson et al., 2012).

2.2.2 *A. cordata*

A. cordata is part of the Betulaceae family and is native to southern Italy (Stevens, 2001). The species is considered to have a small natural range and low genetic diversity (Ducci and Tani, 2009). *A. cordata* is a pioneer species and is regarded as a medium-sized tree with potential to reach heights of 25 m and stem diameter of 65 cm at breast height (Ducci and Tani, 2009). As a pioneer species it has the ability to grow rapidly in forest clearings or clear cuts (Ducci and Tani, 2009). It grows naturally on a wide variety of soil types, with the exception of dry clay soils (Ducci and Tani, 2009). *A. cordata* can be found in coastal areas, tolerating salt air and coastal exposure (Shaw et al., 2014) and is hardy to a maximum of -17 °C (Bannister, 2003).

Its rapid growth potential may make it an ideal candidate for SRF. Trials are underway in Italy as to its potential for bioenergy (Facciotto et al., 2014). However, there have been few field studies of *A. cordata* (Innangi et al., 2017) so comparisons are often made with other species in the genus. Grey alder (*Alnus incana* (L.) Moench) is also known for rapid growth and has been reported to reach maximum current annual increment after 6-7 years in plantations in Sweden (Perttu and Koppel, 1995). Common alder (*Alnus glutinosa* (L.) Gaertn.) has a long leaf retention period which allows it to exploit a long growing season, and along with its ability to rapidly expand its leaf area, makes it a good candidate for biomass production, based on UK data (Leslie et al., 2017).

A. cordata trees establish a symbiotic relationship with *Actinomyces alni* (*Frankia alni*) enabling its roots to fix atmospheric nitrogen, improving soil fertility wherever it grows (Renou-Wilson et al., 2009). Although *A. cordata* is a pioneer species capable of colonising most soil types, it benefits from soil cultivation. In particular height growth and root establishment is reduced on compacted soils compared with ones that have been cultivated (Ducci and Tani, 2009; Sinnett et al., 2008). *A. cordata*

is often planted in mixed stands. A positive effect on growth in common walnut (*Juglans regia* L.) was reported when planted with *A. cordata,* which has been attributed to the effect of nitrogen fixation (Cutini and Giannini, 2009). A similar response has been reported for *Quercus robur* L. when planted in a mixture with *A. cordata* (Battipaglia et al., 2017). This may be advantageous in SRF systems where there may be strong competition for nutrients at higher planting densities (Hall and Burgess, 1990). However, high planting densities may reduce the ability of alder to fix nitrogen, with less photosynthate being allocated to nodules on the roots of *A. rubra* under those conditions compared to trees growing at low planting densities (Bormann and Gordon, 1984).

2.2.3 *P. sitchensis*

P. sitchensis is a conifer species with a native range that stretches along a narrow belt of the Pacific coast from Alaska to California. Introduced into Europe in 1831, the earliest planting recorded in Ireland was in *c*. 1835 (Twomey et al., 2002). *P. sitchensis* has become the main commercial forest species in Ireland and now accounts for approximately 50% of the Irish forest estate (DAFM, 2017). The moist, fertile soils and high atmospheric humidity commonly found in Ireland make it an ideal place for growing *P. sitchensis*.

In conventional forest systems, *P. sitchensis* is a fast-growing species and on favourable sites it often reaches economic maturity in little over 30 years. However, *P. sitchensis* seedlings grow slowly, particularly when planted on afforestation sites, in comparison with other species like poplar or willow (Cannell, 1987). *P. sitchensis* has a low specific leaf area (SLA) which limits the amount of photosynthate produced, slowing the development of leaf area at a young age (Cannell, 1987). Annual height increment rate is slow until it is about six years old, during this period of rapid crown development, after which height rapidly accelerates (Cochrane and Ford, 1978). *P. sitchensis* eventually forms a very efficient, deep layered, dense crown which compensates for the slow leaf area development during its early growth. Once it reaches 6-10 years old, *P. sitchensis* may intercept as much light as poplar (Cannell, 1987) and in closed stands it is a highly productive species (Cochrane and Ford, 1978).

Washington, Oregon and Queen Charlotte Islands (QCI) provenances of *P. sitchensis* are the most frequently used in the Irish planting programme. Washington provenances have performed well in most parts of Ireland while Oregon provenances are better suited to the southern parts of the country (Thompson, 2007). Although QCI provenances has been widely grown in Ireland in the past, the results of research has shown that Washington and Oregon provenances perform better on most sites in Ireland (Thompson et al., 2005). As a result of these findings, Coillte have phased out the use of QCI provenance material since 2006 (Thompson, 2007).

Since *P. sitchensis* is the most productive conventional forest species in Ireland (Farrelly et al., 2009), it is often considered the benchmark for comparing the performance of other species in Irish forestry. Therefore, *P. sitchensis* may have potential as a SRF species, perhaps when planted at closer spacing. Furthermore, stands of *P. sitchensis* grown as a short rotation crop could readily be converted to a conventional crop should market conditions change, providing some flexibility to an owner.

2.3 Planting density

The relationship between growth and planting density depends on the species, growth characteristics, age and growing conditions. It has long been recognised that stand management and planting density can influence resource allocation within and between individual trees (Tomé and Verwijst, 1996). Trees in SRF systems will be harvested earlier in their development than in conventional forestry so it may be advantagous to plant at denser spacings. Most growth and yield tables estimate productivity potential from stand age of 10 onward. There is little information available on the effects of initial competition between trees on growth characteristics and physiological responses. To date most studies have focused on the impact of conventional relatively wide spacings on height, stem diameter and final yield (Benomar et al., 2012; Cannell and Smith, 1980; DeBell et al., 1996). Few studies have investigated the effects of planting densities on crown architecture and biomass allocation (Benomar et al., 2012), particularly during the juvenile period. The planting density chosen will influence establishment costs, wood quality and final yield

(Benomar et al., 2012). The planting densities set out under the Forestry for Fibre scheme for SRF stipulate a minimum of 2,000 stems ha^{-1} (2.0 × 2.5 m). It is likely that this recommendation was based on information derived from conventional forestry systems and may be low for SRF systems. The results from eucalyptus trials in Ireland suggest that between 1,800 (1.9 × 3 m) and 2,000 (2.0 × 2.5 m) plants ha^{-1} may be the optimal planting density over a 12- to 15-year rotation period (Thompson et al., 2012). However, there are few data to confirm that this is the optimal approach for this species (Kerr, 2011; Thompson et al., 2012).

2.3.1 Spacing effects on stem height and diameter

Spacing affects diameter growth more than height growth. Height and stem diameter differences in response to different spacing were evident at an early stage of development (15 and 41 months) in trials of three eucalyptus species in Brazil (Bernardo et al., 1998). High planting density either reduced or had little effect on height growth compared with low planting density (Table 2-1). Tree height increased and stem diameter decreased in *P. sitchensis* as planting density increased in studies carried out in Ireland (Jack, 1971; Lynch, 1981). In addition, crowns grow more vigorously and branches are retained for longer on trees of *P. sitchensis* grown at wider spacing than at narrower spacing (MacDonald and Hubert, 2002), which is probably true of most species. However, the effect of planting density on tree height may change with age. Tree height increased more after 4 years of growth at high than at low planting density in poplar trial in USA, but by year 6 trees planted at a wider spacing were taller (DeBell et al., 1996). Poplar trees, grown at 1×2 m spacing for 2 years were taller with a smaller stem diameter and higher specific leaf area than when grown at 2×3.5 m spacing in France (Toillon et al., 2013).

2.3.2 Spacing effects on crown and root development

Tree crowns vary in shape and size as competition intensity changes (Table 2-1). Significantly fewer resources were allocated into branch production in *E. nitens* grown at closer spacing than those grown at wider spacing (Alcorn et al., 2007; Henskens et al., 2001; Neilsen and Gerrand, 1999). There was little change in tree height in response to spacing with more biomass allocated to diameter growth at the expense

of branches at higher stocking rates in a study in Tasmania in *E. nitens* (Pinkard and Neilsen, 2003). However, a significant reduction in crown depth, branch length and stem diameter were observed as density increased (Neilsen and Gerrand, 1999).

If leaves are unable to intercept enough light to maintain a positive carbon balance (Matyssek and Schulze, 1987), the leaf and ultimately the branch dies (Forrester et al., 2010; Givnish, 1988; Montagu et al., 2003). As planting density increases and consequently competition intensifies, the height to the lowest live branch increases, reducing the overall depth of the live crown. In *A. rubra* and *E. nitens* the live crown depth has been found to decline as planting density increased (Bormann and Gordon, 1984). This was also the case with *E. pilularis* and *E. cloeziana* after 4 years of growth in the field (Alcorn et al., 2007). However, tree height and height to lowest live branch did not change in *P. sitchensis* as planting density increased, but there was a significant decrease in leaf dry weight (Simpson and Denne, 1997). The number of branches per whorl declined as planting density increased in *P. sitchensis* (Jack, 1971). The practice of increasing stocking density to improve stem wood quality has been widely used (Alcorn et al., 2007; Mäkinen and Hein, 2006; Neilsen and Gerrand, 1999). However, total biomass is of primary interest in SRF systems. Therefore, species with rapid early growth irrespective of branch numbers may be more important for SRF systems.

Stand density tends to increase variation in plant size (Weiner, 1988). If water or nutrient availability is limited more growth is allocated to roots than to shoots. If light availability is limited more photosynthesis is allocated to shoot growth than root growth (Poorter et al., 2012). The degree of competition between neighbouring plants for the same above- and below-ground resources varies with species, site and environmental conditions (light, water or nutrients) (Donald, 1958). Therefore, planting density can affect above- and below-ground competition through its effect on the demand for resources.

Transpiring foliage requires an appropriate balance between the amount of root tissue needed to absorb soil water to offset the transpiration losses (Bernier et al., 1995). Therefore, trees must have a root-to-shoot ratio that favours a positive water balance. In most mature trees, under normal conditions, the root: shoot ratio is stable,

with values ranging from 0.16 to 0.20 (Harris, 1992). In general the root: shoot ratio will decrease with stand age (Saint-André et al., 2005) and is affected by tree size and species (Konôpka et al., 2010). Trees grown at wider spacing had a larger root: shoot ratio than those grown at close spacing in *A. rubra* and *Populus* hybrids in Scotland (Proe et al., 2002) and *E. camaldulensis, E. urophylla* and *E. pellita* in Brazil (Bernardo et al., 1998). Shoot growth declined as planting density was increased three years after planting, but root growth was not affected, in a study of poplar carried out in Canada (Benomar et al., 2012). Shade tolerant conifers, such as spruce and fir, have a lower root: shoot ratio than shade intolerant species such as pines (Messier et al., 1999).

2.3.3 Crown and leaf structure

Crown architecture influences tree growth through its effect on leaf distribution and light interception (Binkley et al., 2013). The vertical distribution of leaves and their photosynthetic properties depend on species type, the leaf structure and angle of the leaf to irradiance within the crown, as well as the levels of acclimation to shade conditions (Hikosaka et al., 2016; Isebrands and Michael, 1986; Isebrands and Nelson, 1982). A high planting density will result in the production of a greater proportion of shade leaves within the canopy (Pons, 2016). Therefore, any study of photosynthetic properties of a species in relation to planting density must consider the difference in light levels permeating the crown.

2.3.4 Specific leaf area and leaf area index

Specific leaf area (SLA) is the ratio of leaf area to leaf dry mass. The total leaf area and its effect on light interception and light use efficiency influences crown expansion and growth. SLA tends to decline with stem height. Needles which formed high in the crown (sun leaves) in *P. sitchensis* had a lower SLA than needles formed lower down (shade leaves) (Norman and Jarvis, 1974). Similarly, SLA was higher in shade leaves than sun leaves in Norway spruce (*Picea abies*) (Urban et al., 2012). SLA declined with stem height in *A. incana* (Perttu and Koppel, 1995) and *Salix viminalis* (Verwijst and Telenius, 1999), *E. nitens* (Pinkard and Beadle, 1998) and *E. cloeziana* and *E. pilularis* (Alcorn et al., 2013). Species with high SLA tend to have a higher leaf-level rates of photosynthesis per unit leaf mass (Poorter and Evans, 1998). Therefore, species with a

high SLA, which is not negatively affected with increasing planting density, could be a suitable candidate in SRF systems.

Trees planted in SRF systems at high density are characterised as having rapid rates of canopy closure and high leaf-area index values (Ceulemans and Deraedt, 1999). The amount and arrangement of foliage in its crown determines the amount of light a tree can harvest (Linder and Flower-Ellis, 1992) which can be quantified with leaf area index (LAI). LAI characterises the size or area of the crown or canopy, greatly affecting photosynthetic potential (Barclay, 1998) and productivity (Beadle, 1997). Watson (1947) defined LAI as the total one-sided area of photosynthetic tissue per unit ground surface area. Although a morphological measure, it is often used in ecophysiological studies (Behera et al., 2010), especially in the process of scaling up from leaf to canopy level (Bréda, 2003). Canopy closure is a gradual process. As trees grow in a stand the branches from neighbouring trees begin to overlap and compete for light and other resources (Tabbush and White, 1988). The competition between trees in square planting schemes is considered to be underway once projected crown area exceeds the distance between the planting space, which is when the crowns begin to overlap (Radtke and Burkhart, 1999). Maximum LAI for a species is achieved over time under optimum growing conditions and reflects the ability of the shaded lower leaves to intercept sufficient light to maintain a positive carbon balance, otherwise the leaves senesce and fall (Beadle, 1997). For a given species silvicultural treatments, site and environment, fertilization, irrigation and thinning affect LAI (Medhurst and Beadle, 2001).

The difference in a species crown configuration and the speed with which it achieves high or maximum LAI affects its productivity. Clones of poplar that had the largest leaves and highest LAI generated the highest rates of photosynthesis, resulting in higher yields than in other clones in trials conducted in France (Barigah et al., 1994). Most of the branches, except at the top of the crown, are displayed horizontally and the branching structure is regular in *P. sitchensis* (Norman and Jarvis, 1974). The efficient branching structure, combined with a relatively long needle retention period (≥4 years), allows it to achieve a high leaf area index (Norman and Jarvis, 1974). Leaf area may differ seasonally. *A. glutinosa* sheds some leaves in July, with the main

litterfall occurring in October in the Nederland's (Witkamp and Van der Drift, 1961). In general alders (as with most deciduous temperate trees) tend to hold most leaves in the upper crown (Čermák, 1989). The leaves in *A. glutinosa* are largely held in horizontal layers, achieving a maximum LAI of c. 4.8 (Eschenbach and Kappen, 1996). The vertical distribution of leaves is skewed towards the top of the crown in *E. nitens* and it achieves a LAI of between 4.0 and 4.9 (Medhurst and Beadle, 2001). LAI would appear to be relatively constant, irrespective of spacing, once canopy closure has occurred (Pinkard and Neilsen, 2003), with most light being intercepted (95%) at LAI of 4.0 in *E. nitens* (Pinkard et al., 1999).

2.3.5 Spacing effects on wood density

The characteristics of wood change with tree age and the position in the stem (Larson et al., 2001). Wood production in a tree may be separated into crown or core wood and mature wood (Barbour, 2004). Crown or core wood is commonly defined as the zone of wood extending outward from the pith (wood produced when that part of the stem was close to live branches) and upward into the crown of an older tree (Larson et al., 2001). Mature wood is found in the outer layers near the bark (Burley et al., 2004). Wood density within a tree varies from pith to bark and with height in the stem (Treacy et al., 2000). Wood density is a complex characteristic which is affected by the thickness of cell wall, the cell diameter, the chemical content of the wood and the early- to late-wood ratio (Cave and Walker, 1994). The pattern of change in wood density also varies with species (Larson et al., 2001). Faster growth rates generally result in the production of wood with wider rings and consequently lower wood density (Williamson and Wiemann, 2010). Mature wood is composed of cells that have a relatively small diameter and a thick cell wall and therefore a higher density than core wood, which has larger cells and thinner cell walls (Bowyer et al., 2007). Large vigorous crowns produce more core wood than mature wood. The ratio of core to mature wood will vary with species and the silvicultural practices applied (Barbour, 2004). In general the longer the rotation period the lower the core wood content and the stronger its mechanical properties (Bao et al., 2001). Encouraging faster growth

and shorter rotations is likely to result in a larger core of lower density wood (Brazier, 1977).

Wood density will affect biomass yield and is an important factor in biomass utilization (Brazier and Howell, 1979). Wood density is approximately proportional to calorific value (Neilan and Thompson, 2008). Selection of species which have a higher-density wood or wood of high calorific properties would be beneficial to SRF systems. Wood density varies between species, with provenances within a species (Zobel and Van Buijtenen, 1989), sites, trees within sites and management regimes (Fearnside, 1997; Murphy and Pfeifer, 2002).

Faster growing southerly provenances of *P. sitchensis* (Washington or Oregon) tend to have a lower wood density (379 and 382, respectively) than more northerly provenances (QCI 401 kg m^{-3}) (Jeffers, 1959; Murphy and Pfeifer, 2002). Plant spacing and the age of the tree affect wood density (Barbour, 2004). Wood density in *P. sitchensis* at age 48 years was higher at closer spacing (364 kg m^{-3} at 0.9×0.9 m) than at wider spacing (321 kg m^{-3} at 2.4×2.4 m) in Norway (Petty et al., 1990). Wood density of *P. sitchensis* grown in Ireland was estimated to be 475 kg m^{-3} at 9 years and decreased with age to 365 kg m^{-3} at 46 years (Tobin and Nieuwenhuis, 2007). It is therefore possible to achieve a higher wood density at higher planting density over a short rotation in *P. sitchensis*. Wood density in *P. sitchensis* was higher at DBH than higher up the stem (Simpson and Denne, 1997); however, it did not differ at DBH for trees grown at different spacing (Deans and Milne, 1999). Although *P. sitchensis* has a relatively slow growth rate during the early growth period compared to *E. nitens,* its wood density is comparable to eucalyptus.

Compared to some eucalypts, *E. nitens* has a relatively low wood density (Neilan and Thompson, 2008), varying from 414 to 454 kg m^{-3} in 5 to 17 years old material (Lausberg et al., 1995; Senelwa and Sims, 1999; Thompson et al., 2012). Wood density varied from 492 to 600 kg m^{-3} at 9 years of age in *E. globulus* (Miranda et al., 2001). Wood density tends to increase with stem height in eucalyptus, which is the opposite of that observed in *P. sitchensis* (Van Wyk, 1983).

No published data were found for wood density in *A. cordata*. The wood density for other species of alder ranges from 430 kg m^{-3} for *A. japonica* to 380 kg m^{-3}

for *A. jorullensis* and *A. ferrruginea* (Reyes et al., 1992). In Ireland, air-dried *A. glutinosa* had a wood density of 500 kg m^{-3} (Knaggs and Xenopoulou, 2004).

2.3.6 Stand biomass production

Stocking density often affects individual tree growth due in part to the same resources being shared between more plants (Thoranisorn et al., 1990). However, the overall impact on stand production is important for SRF. The quantity of stand biomass may increase due to the larger numbers of stems planted, such as that observed in *E. camaldulensis* (Thoranisorn et al., 1990), *E. nitens* (Pinkard and Neilsen, 2003) and *A. rubra* (Bormann and Gordon, 1984) stands. In a trial planted at very high planting densities, yields of 48 and 88 t ha^{-1} at 0.12 × 0.12 m and 0.27 m × 0.06 m spacings after 3 years of growth were reported for *P. sitchensis* in Ireland (McCarthy, 1979). Although planting at a high density resulted in greater yield in that study, McCarthy concluded that little additional biomass would be produced over a longer rotation, but the cost of stocking at this high a density was considerable.

2.3.7 Rotation length

The rotation period is the time from planting to harvesting of forest trees, and unlike conventional forests, trees in SRF systems are harvested early in their development to take advantage of the rapid juvenile growth period. The rotation depends on the species, site conditions and stem diameter at the time of harvesting and silvicultural system used. SRF is generally used to provide an energy crop over a short period of time (Crow, 2011). In comparison with agricultural crops, forest species often have slow annual production rates and only reach maximum annual increment after c. 15 years growth (McCarthy, 1979).

Table 2-1 Examples of published spacing trials of fast-growing species, listing the impact of higher planting density on crop morphology. Trials included a variety of management systems (SRF, SRC). The locations of the trials and age of assessment are also noted.

Species	Spacing	Location	Effect of high planting density on tree growth	Trial (age)
E. pilularis *E. cloeziana*	1.5×2 m, 2×3 m and 2×4 m	Australia	Height decreased DBH decreased Crown depth decreased (Alcorn et al., 2007)	Spacing Branching (4)
E. globulus	2×4 m, 2×10, 10×10 m	Australia	Height unchanged Stem diameter decreased Leaf area decreased Branch number and size decreased Stand volume increased (Henskens et al., 2001)	Spacing Branching (4)
E. nitens	2×3 m and 4×5 m	Tasmania	Height unaffected DBH increased Branch length and diameter decreased Leaf area decreased Live crown depth decreased Stand level biomass increased (Pinkard and Neilsen, 2003)	Spacing (7)
E. nitens	2×3 m, 2,5×3 m, 3×3.3 m, 2.5×4 m, 3×4 m, 4×5 m	Tasmania	Height unaffected Stem diameter decreased Branch length decreased Crown depth decreased Stand volume increased (Neilsen and Gerrand, 1999)	Spacing Branching (5)
E. camaldulensis, *E. urophylla* *E. pellita*	3×1.5 m, 3×3 m, 4×3 m	Brazil	Height unchanged Stem diameter decreased Leaf area decreased Tree biomass decreased Stand biomass increased Root biomass decreased (Bernardo et al., 1998)	Spacing Biomass (15, 31 and 41 months)
E. camaldulensis	0.5×0.5 m, 0.7×0.8 m, 1×1 m, 1.5×1.5 m, 1.6×2.5 m, 2×4.5 m, 4×4 m	Thailand	Height decreased Stem diameter decreased Tree volume decreased (Thoranisorn et al., 1990)	Spacing Thinning (1-6)
Populus hybrids	0.5×0.5 m, 1×1 m, 2×2 m	USA	Height increased <4 years Height decreased >4 years Stem diameter decreased Stand basal area increased Stand biomass decreased (DeBell et al., 1996)	SRC (4-7)
Populus hybrids	1×2 m, 2×3.5 m	France	Height increased Height unchanged (Water deprived) Stem diameter decreased (Toillon et al., 2013)	SRC (2)

Continued...

Species	Spacing	Location	Effect of high planting density on tree growth	Trial (age)
Populus clones × 2	1×1 m, 3×3 m, 5×5 m	Canada	Height decreased (Clone 1), increased (Clone 2) DBH decreased (Clone 1) unaffected (Clone 2) Above-ground biomass ha^{-1} increased Root biomass unchanged (Benomar et al., 2012)	SRC (6)
Populus clones x 3	2×4 m, 3×4 m, 4×4 m, 4×5 m,	China	Height unchanged Stem diameter decreased (Fang et al., 1999)	SRC (6)
Alnus rubra (Bong) *P. balsamifera var. Michauxii* (Henry) × *P. trichocarpa var. Hastata* (Dode) Farwell *Salix* (Bowles hybrid)	1.0×1.0 m and 1.5×1.5 m 1.0×1.0 m (Salix)	Scotland	Coppicing reduced Alnus and Poplar biomass Higher density increased biomass 35% (Proe et al., 2002)	SRC (5)
Betula pendula (Roth) *Acer pseudoplatanus* (L. Tintigny) *Populus trichocarpa × deltoids* (Hoogvorst) *Salix viminalis* (Orm)	1.0×1.5 m 1.0×1.5 m 1.0×0.5 m 1.0×0.5 m	France and Belgium	Assessment of biomass per species with *populus* and *salix* producing the higher quantities (Vande Walle et al., 2007)	SRF (4)
Populus clones *Salix* clones	Various trials from 0.7×0.7 m to 1.4×1.4 m	UK	Biomass reduced between 1st and 2nd rotation (Mitchell et al., 1993); (Mitchell et al., 1999)	SRC (3-5)
Salix sp. *P. trichocarpa cv. Muhle* Larsen) *P. tremula × tremuloides* cv. Astria	2.0×0.3 m, 2.0×0.6 m, 2.0×1.0 m	Germany	Biomass varied with species, site and fertilization treatment (Hofmann-Schielle et al., 1999)	SRC (5 - 10)
A. rubra	0.61×1.22 m, 1.22×1.82 m, 2.74×2.74 m	USA	Height unchanged DBH decreased Crown volume decreased Stand volume increased (Bormann and Gordon, 1984)	Spacing (5)
Picea sitchensis *Pinus contorta*	1.2×1.2 m to 3.6×3.6 m	Ireland	Height increased Stem diameter unchanged Stand volume increased (Lynch, 1981)	Spacing Thinning (9)
Pseudotsuga menziesii (Mirb.) Franco var. *menziesii*	1×3.5 m, 1.5×5 m, 5.5×6 m	USA	Height increased to year 5 then decreased DBH increased to year 5 then decreased (Woodruff et al., 2002)	Spacing (8 - 12)
Pinus taeda	1.5×1.5 m, 1.5×1.8 m, 1.4×2.5 m, 1.8×2.5 m, 2×3.5 m, 3×4.5 m	USA	Height unchanged DBH decreased (Will et al., 2005)	Spacing (4)

A review of SRF systems suggested a target of 15 cm diameter at breast height (DBH) over a rotation of 8-20 years for single-stemmed trees (McKay, 2011). The relatively short rotations of a SRF system are resource demanding and not all soils can support such a system (de Franchi et al., 2010). The degree of competition in a stand will also depend on the nature of the interaction between trees, e.g. their size relative to surrounding trees and stocking density (Bella, 1971; Tomé and Burkhart, 1989). Biomass targets over short rotations might only be achieved at higher densities (McCarthy, 1979).

Natural self-thinning takes place as the trees grow and competition for light, water and nutrients increases (Hikosaka et al., 2016) and smaller plants die due to suppression by larger more dominant neighbours. In the natural environment the process of self-thinning occurs throughout the life of a forest (Peet and Christensen, 1987). Mortality due to competition is initially low in plantation forests, increasing gradually as self-thinning occurs, mostly after canopy closure. In conventional forestry, stands are usually thinned to avoid such losses. At higher planting densities the process of self-thinning will begin earlier as less dominant trees become shaded and competition for light increases (Thoranisorn et al., 1990). Self-thinning began once canopy closure occurred, at 12 – 16 years old in Norway spruce (Konôpka et al., 2015). Self-thinning began earlier and a smaller mean tree size was produced after 5 years growth in *E. camaldulensis* grown at high density (0.5×0.5 m) compared with low density (4×4 m) (Thoranisorn et al., 1990). Successful production of biomass from SRF systems must combine a planting density which does not result in excessive self-thinning before the end of a rotation period. Such planning requires data on planting density and productivity for each species selected. The objective in short rotation systems is to delay the onset of self-thinning to maximise productivity. Therefore, a planting density that allows trees to attain a specific minimum size before competition-related reductions in growth rate and mortality occur is required (DeBell et al., 1996).

2.3.8 Physiology and productivity

The amount of light that a tree harvests largely determines tree growth through the process of photosynthesis, which fixes atmospheric carbon and produces carbohydrates used for respiration and growth (Bernier et al., 2003). Two processes occur: light interception (*I*) by the leaves and the CO_2 assimilation (P_N) within the leaf. Sun and shade leaves tend to respond differently to light availability which may vary with planting density (Michael et al., 1990).

There is a strong relationship between net photosynthesis, leaf area and biomass production (Barigah et al., 1994). A direct linear relationship has been found between irradiance and biomass production in studies in Scotland, USA and Sweden (Leverenz and Hinckley, 1990; Linder and Flower-Ellis, 1992) and although the relationship is robust in young plants (Barigah et al., 1994), it is more complex than a simple linear relationship would imply (Agren et al., 1991; Barigah et al., 1994). Adverse climatic conditions and stress levels etc., may limit photosynthesis rates (Long et al., 1996) which may vary with site and management conditions.

Photosynthetic capacity has been positively correlated with biomass production in a range of species including *Pinus taeda* (L.) (Boltz et al., 1986), poplar (Ceulemans and Impens, 1983; Michael et al., 1990), *Larix decidua x leptolepis* (Matyssek and Schulze, 1987) and 12 Brazilian rainforest species (Lusk and Pozo, 2002). However, other authors reported a low correlation between biomass production and photosynthesis rates in poplar (Gifford and Evans, 1981; Okafo and Hanover, 1978; Reighard and Hanover, 1990). A number of reasons can be advanced to explain the conflicting results. The characteristic of the leaves selected for study may have affected the outcomes. Photosynthesis rates will vary with genotype, crown position and season (Barigah et al., 1994) which might explain some of the differences reported in the selection of measurement points (Medhurst et al., 1999). Treatment effects may not be manifested if the selected leaves are not comparable, such as due to differences between sun and shade leaves.

An objective and repeatable selection process has been developed in an effort to address the effect of leaf selection bias, known as the plastochron index (PI) (Erickson and Michelini, 1957). An index can also be used to identify and compare

leaves of similar maturity based on the order and position of the leaf from the stem or branch apex. As the development of the plant can be indirectly related to time, the index enables rapid and repeatable selection of morphologically and physiologically equivalent material (Erickson and Michelini, 1957; Hill and Lord, 1990).

2.3.9 Photosynthesis

Photosynthetically active radiation (PAR) in the wavelengths between 400-700 nm is used in photosynthesis. The rate of photosynthesis is largely determined by the amount of PAR absorbed by the leaves and the efficiency with which the light is harvested and converted into biomass (Taiz and Zeiger, 2010). The quality and quantity of light absorbed by leaves, the amount of photosynthate allocated to different tissues in the tree will affect the efficiency of the generation of biomass. Production potential will also differ with species and the environment in which the trees are growing (Binkley et al., 2013; Ceulemans et al., 1996). The structure of a canopy affects evapotranspiration, radiation interception and penetration, and the productivity of a stand (Behera et al., 2010). Higher planting densities will intensify competition between the individual tree crowns, increasing the density of the overall canopy. Decreasing light availability within a crown causes leaf acclimation, resulting in changes in leaf mass, leaf nitrogen content and chlorophyll content. A plant will alter leaf area and light harvesting capacity, affecting the photosynthetic capacity of the crown as a whole (Niinemets, 2016).

Trees detect competition through changes in the spectral composition of light on foliage, mainly in the red: far-red ratio (R: FR). Leaf chlorophyll content (Ch_{leaf}) declines as stress increases, which affects the absorbance of FR. The ratio decreases as the intensity of shade within the crown increases, with the amount of absorption of R increasing compared to FR (Pons, 2016). Shade leaves receive a lower quantity of light, which is detected through the phytochrome system which down-regulates photosynthetic capacity and can induce senescence (Pons, 2016). Shade leaves often contain more chlorophyll (Ördög and Molnár, 2011; Taiz and Zeiger, 2010) than sun leaves as more thylakoids are stacked higher in wider grana. The redistribution of chloroplasts within the cytosol allows plants to respond to light intensity depending on

whether light harvesting needs to be increased or decreased. However, Ch_{leaf} differs between species. Ch_{leaf} was higher in sun leaves than shade leaves of *Alnus hirsuta* ((Spach) Rupr.) and *Juglans ailanthifolia* (Carrière) while in the same study Ch_{leaf} was higher in shade leaves than sun leaves of *Fraxinus mandshurica* var*. japonica* (Rupr), *Betula platyphylla* var*. japonica* ((Miq.) Hara) and *Ulmus davidiana* var*. japonica* (Koike et al., 2001).

There are several methods for measuring chlorophyll concentration in leaves. Chlorophyll can be extracted from leaves and Ch_{leaf} calculated in a laboratory, but indirect methods using a chlorophyll meter provide sufficiently accurate information, can be carried out quickly and do not involve the destruction of leaf material. This meter works on the principle that there is a linear relationship between fluorescence (F) emission ratio of red: far-red F735/F710 and Ch_{leaf} in the range 41 to 675 mg m^{-2} (Gitelson et al., 1999). It is this ratio that is used in the measurement of chlorophyll content in leaves.

Photosynthesis is sensitive to environmental conditions (Bond, 2000). Photosynthesis, respiration, and consequently root, shoot, branch and leaf growth, depend on the availability of light, water and nutrients (Ryan et al., 2010) as well as suitable environmental conditions. Light use efficiency within the crown affects productivity (Monteith and Moss, 1977), but the availability of water and nutrients determines the effectiveness of the forest canopy (Linder and Flower-Ellis, 1992). The photosynthetic capacity of leaves is related to their nitrogen content. The proteins of the thylakoids used during the Calvin cycle hold the bulk of leaf nitrogen, i.e. thylakoid nitrogen is proportional to the chlorophyll content (50 mol thylakoid N mol^{-1} Chl) (Evans, 1989). The rapid early growth and high density planting potentially required in a SRF system production may result in the depletion of the nitrogen in the soil (Gower et al., 1996) thus affecting productivity.

Photosynthetic rates are controlled through the amount of PAR intercepted, leaf area, shape and size (Taiz and Zeiger, 2010); and leaf orientation, crown position, and plant branchiness (Isebrands and Michael, 1986; Isebrands and Nelson, 1982). Planting density can affect all of these responses. Leaves that are shaded will receive a different quality of light, at a lower light intensity level than sun leaves (Taiz and

Zeiger, 2010). Leaves acclimate to the environmental conditions, so as a tree grows the newly produced leaves may have different morphological and biochemical characteristics than those produced during earlier development (Taiz and Zeiger, 2010). As a leaf ages or as growing conditions change, the biochemical conditions within the leaf are affected (Spencer and Titus, 1972). Changes to the morphological characteristics affect light interception per unit leaf area: i) at tissue level, the light intercepted per unit chlorophyll; ii) at leaf level, the exposure of a single leaf and; and iii) at crown level the leaf area and arrangement on shoots and branches (Niinemets and Sack, 2006). In comparison with other countries, light levels in Ireland are low due to frequent cloud cover and lower sun elevations related to the geographic position (Patenaude et al., 2005). However, overall photosynthetic rates may not be limited, with the mild oceanic climate and low moisture stress providing excellent growing conditions such that many of the conventionally managed forests in Ireland have among the highest productivity in Europe (Tobin et al., 2018). It has generally been assumed that in low light environments plants at higher planting densities (most of the crown of a tree is in some degree of shade) are strongly limited by light availability. However, a plants response to nutrient availability, plays a greater role in light-limited environments through their effect on metabolic processes that affect light harvesting (Baltzer and Thomas, 2005).

2.3.10 Crown structure and light interactions

The ability of the leaves of a tree to acclimate to low light levels at high density planting will affect species' productivity potential. Sun leaves have a higher maximum net photosynthesis rate than shade leaves in *P. sitchensis* (Leverenz and Jarvis, 1979). However, the crown of *P. sitchensis* is evenly structured with a regular vertical distribution of branches and needles, which ensures that light penetrates efficiently to the lower crown (Cannell, 1987; Norman and Jarvis, 1974). The structure of the *P. sitchensis* canopy allows good air circulation, such that CO_2 levels do not decline greatly compared with ambient levels above the canopy. There are greater declines in most other tree species and agricultural crops. Therefore, *P. sitchensis* trees can maintain high photosynthetic rates over a large proportion of the crown, thus resulting

in a higher quantum efficiency than in most broadleaved trees (Cannell, 1987). Thus the shaded foliage makes a considerable contribution to the total photosynthesis in *P. sitchensis* (Cannell, 1987). However, it generally takes *P. sitchensis* trees 6-8 years to build up an efficient canopy, so initial productivity may be low during this period (Cochrane and Ford, 1978).

E. nitens grows naturally in the dry interior of Australia and produces both ovate and lanceolate leaves during the juvenile period. Vertical leaves reduce the midday heat loads thereby increasing water use efficiency (King, 1997). However, vertically-angled leaves, as found in the mature crowns of *E. nitens,* may increase the competitive advantage of this species compared with other species, allowing it to intercept light from the sun at low elevation at high latitudes (King, 1997), such as in Ireland. The pendulous nature of the crown of *E. nitens* allows a greater proportion of incident light to penetrate the canopy (Tausz et al., 2005).

There is little published information available on the physiology of alder, and in particular on *A. cordata*. Spacing did not affect the net photosynthesis in the upper sun leaves of the crown in *A. rubra* (Proe et al., 2002). However, more widely spaced trees had higher photosynthesis rates in the lower crown than those planted at narrow spacing. Therefore, planting alder at higher densities may have implications for crown photosynthesis rates.

2.4 Prediction of growth and yield

The growth and yield of forest stands can be predicted with models using either empirical modelling and process-based approaches (Korzukhin et al., 1996; Mendoza and Vanclay, 2008). An empirical modelling approach is possibly the simplest method of predicting forest growth, but it assumes climatic and growing conditions will remain constant (Pinjuv et al., 2006). Forest growth behaviour can be more precisely predicted using empirical models providing the conditions which are used for calibrating the model are very similar to the conditions to which the model is being applied (Korzukhin et al., 1996). However, the highly changeable nature of forest ecosystems can render accurate predictions difficult with empirical modelling. The first simple empirical models developed were yield tables.

Many empirical models have since been created; CANTY was developed by the New Zealand Forest Research Institute (1991) as a stand-level growth and yield model for pine plantations in New Zealand (Goulding, 1995); GrowFor is another empirical stand-level model used in Ireland since 2005, particularly for *P. sitchensis* (Broad and Lynch, 2006). It was modified from models developed for even-aged stands of *Pinus radiata* (Garcia, 1984). It has since been developed to include models for ash (*Fraxinus excelsior* L.) and Japanese larch (*Larix kaempferi* (Lamb.) Carrière) (McCullagh, 2013).

Process-based models are generally constructed to estimate plant responses to environmental changes. They are mathematical representations of biological systems incorporating ecological and physiological mechanisms in response to changes in stressors or resource availability (Johnsen et al., 2001). The data used in a process-based model must be general enough (for different site conditions, tree age etc.) to be applicable to the new conditions being tested (Korzukhin et al., 1996). Although the same data may be used in both models, a process-model describes the data using mechanisms or processes that affect an outcome. Process-models are designed to investigate the functioning of the mechanisms and relationships affecting forest growth (Bernier et al., 2003). They can predict the responses to resource, silvicultural practices and site limitations. A practical process-based model should be capable of using information readily accessible and not require highly complex and difficult-to-measure data describing canopy dynamics (Bernier et al., 2003). Numerous process-based models have been developed for use in forest ecosystem applications, including the ECOPHYS model which was designed to model morphological and physiological factors affecting growth of juvenile clonal poplar (Rauscher et al., 1990) and the CABALA (carbon balance process-model) designed to provide silvicultural decision support for *E. globulus* plantations (Battaglia et al., 2004).

There are many hybrid models, which use a combination of both approaches (Korzukhin et al., 1996; Pinjuv et al., 2006), incorporating environmental influences with empirical growth and yield data, such as 3-PG (Landsberg and Waring, 1997); FOREST-BGC (Running and Coughlan, 1988); and PROMOD (Battaglia and Sands, 1997). Various hybrid and process-based models could be used to simulate growth for SRF. The 3-PG (physiological principles predicting growth) model was developed for use in

research and was designed for generic application to any site or species (Landsberg et al., 2003), as described in more detail below.

2.4.1 The 3-PG model

The 3-PG model was developed by Landsberg and Waring (1997) as a generalized model of forest productivity, which uses as data inputs radiation-use efficiency, carbon fluxes and biomass partitioning. It simulates the growth of intensively managed stands (Sands and Landsberg, 2002) and requires parameterisation of each individual species as well as data for the local climate.

The high degree of natural variation in growth rates in eucalyptus species (Campoe et al., 2012; Neilsen and Gerrand, 1999) may make modelling of eucalyptus production difficult. Nevertheless, the 3-PG model was first used to predict the growth of *Eucalyptus globulus* (Sands and Landsberg, 2002). The 3-PG model itself, along with input data and parameterization values, have provided a base-line for modellers, with many default values being applicable to other species (Landsberg et al., 2003). Predictions made using 3-PG were more accurate than an empirical approach in predicting diameter at breast height (DBH), stand volume and foliar biomass *in E. nitens* in Spain. This model was used to forecast the impact of thinning and rotation lengths on biomass yield (Pérez-Cruzado et al., 2011). 3-PG accurately predicted mean annual increment, total stand volume, basal area, DBH, leaf area index (LAI) and the availability of soil water in clones of *E. grandis* in Brazil, (Almeida et al., 2004). It was also used to evaluate the effects of variations in soil and climate to assess site suitability for growing *E. nitens* in Chile (Rodríguez et al., 2009). The potential productivity of *E. nitens* as a bioenergy crop in Spain was predicted using the 3-PG model (González-García et al., 2016). The model provided a reasonable estimate of above-ground biomass and water use when compared with observed data when used to evaluate the long-term growth of stands using various stocking densities and rotation lengths.

The 3-PG model has been used to investigate climatic limitations for species in particular regions. For sites in the UK the model predicted that low temperatures would reduce photosynthesis and growth in *P. sitchensis*, whereas drought or vapour

pressure deficits would not affect development. Waring (2000) used the 3-PG model to estimate the growth limitations of the species in the UK. In comparison with 3-PG model-generated estimates, empirical growth models more poorly represented regional growth differences in Scottish-grown *P. sitchensis* (Minunno et al., 2010)

To this authors knowledge there is no published information available on the application of the 3-PG model to estimate growth or productivity of *A. cordata* or any of the *Alnus* genus. However, the 3-PG model has been used to estimate the gross primary productivity of deciduous forests using a set of standard values to predict the growth of *Betula platyphylla* (Sukaczev) in Japan (Potithep and Yasuoka, 2011) and hybrid poplar in Canada (Amichev et al., 2010). The resulting predictions were accurate when compared with empirical data. Overall the 3-PG model has proven to be an accurate predictor of growth and productivity once parameterisation is correctly applied.

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3 The effect of planting density on morphological and physiological responses in *Eucalyptus nitens, Alnus cordata* and *Picea sitchensis*.

3.1 Abstract

The morphological and physiological responses of shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) to changes in planting density were investigated over a 10-month period in a polytunnel, with the aim of identifying the characteristics most affected by competition. The trees of each species were planted into pots at densities of 1, 4 or 8 trees per pot. The pots were placed in an unheated polytunnel from March 2015 to February 2016. Tree height, stem diameter, branch length and number, leaf area and leaf dry weight, leaf area index, leaf chlorophyll concentration (Ch_{leaf}) and photosynthesis rates (P_N) were measured periodically. Above- and below-ground biomass was determined at the end of the experiment period. *E. nitens* maintained a shallow crown with a low proportion of shade leaves at all planting densities. Ch_{leaf} and P_N decreased as planting density increased. The rate of shedding in lower leaves and branches increased as planting density increased. *A. cordata* produced a large vigorous crown with long branches. Branch length declined significantly as planting density increased. Ch_{leaf} and P_N declined as competition increased, and although P_N was lower than in *E. nitens*, *A. cordata* produced the highest biomass of the three species at all planting densities. *P. sitchensis* was the least vigorous of the three species. However, it produced a dense crown and the highest root-to-shoot ratio at all planting densities. There were also significant differences in leaf area and dry mass with planting density in *P. sitchensis*. Total biomass declined with increasing planting density in all species. The most sensitive growth characteristics to planting density were root collar diameter, branch length, leaf area and leaf dry weight. Ch_{leaf} and P_N of shade leaves of all species were considered the most useful characteristics for assessing the effects of competition under field conditions.

3.2 Introduction

Planting density can affect tree physiological activity (and ultimately stand productivity) through competition for resources including light, water and nutrients (Benomar et al., 2012; Toillon et al., 2013). Knowledge of the physiological mechanisms which control tree growth is essential in optimising productivity for forest management. Effects of competition and other stresses can be identified through comparison of measurements of stem, branch, leaf and root characteristics. When soil conditions are favourable and with sufficient water and nutrients, inter-tree competition will mainly be for light. Although competition in a stand may occur early in a rotation the impact may not be apparent morphologically until much later. However, the competition which manifests during early growth may have implications for productivity later in the rotation.

Three species were selected for study because of their known potential as short rotation forestry (SRF) species (Chapter 2.2) and because they have quite different growth strategies. Shining gum eucalyptus (*Eucalyptus nitens* (Deane & Maiden) Maiden) is known for fast growth rates in Ireland and for the high calorific value of its timber (Thompson et al., 2012). Italian alder (*Alnus cordata* (Loisel.) Duby) is known for its ability to exploit a long growing season and is recommended by DAFM for use in the Forestry for Fibre scheme (DAFM, 2018) but its growth characteristics or potential yield have not been well documented. Sitka spruce (*Picea sitchensis* (Bong.) Carrière) was selected because of its fast growth and high density wood (Treacy et al., 2000). It is also the most productive and widely planted forest species in Ireland (Farrelly et al., 2009) and is considered the benchmark for comparing other species. However, there is little information on the potential for using *P. sitchensis* as a SRF species.

It has been well documented that planting density will influence, either negatively or positively, stem height and diameter (Table 2-1). Variation in growth responses will depend on species, spacing and age at which measurements were taken. For example, when planted at higher density, stem height increased but there was no change in stem diameter after 9 years in *P. sitchensis,* (Lynch, 1981). Height was not affected and stem diameter decreased at the higher planting densities at 5-7 years growth in *E. nitens* (Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003). Tree

height did not change and stem diameter decreased at 5 years when the planting density was increased in *A. rubra* (Bormann and Gordon, 1984). Planting density also affected branch length, branch diameter, crown height, leaf area and leaf dry weight (Table 2-1). However, few if any of these traits have been assessed during very early stages of stand development.

Canopy closure is a gradual process. As trees grow in a stand the branches from neighbouring trees begin to overlap and compete for light and other resources (Tabbush and White, 1988). Higher density planting ensures that canopy closure will occur sooner in the rotation and that stand leaf area will increase at a faster rate. The ratio of sun to shade leaves within the crown of each tree may also change. Sun and shade leaves tend to exhibit different responses to stress across different planting densities (Michael et al., 1990). The position of a leaf within the plant crown and stand canopy affects its light environment, its rate of net CO_2 uptake and its photosynthetic efficiency (Boardman, 1977). Therefore, assessments of photosynthetic rates, chlorophyll concentration and specific leaf area may reveal important information about tree responses to different planting densities.

The aim of this study was to assess the effects of planting densities on the growth and physiological responses of three species potentially suitable for SRF in Ireland. A polytunnel experiment was used to assess the effect of planting density on growth and physiological responses while minimising other potentially confounding environmental effects. The specific objectives of the study were to:

- assess the effect of planting density on individual tree physiological growth responses;
- develop methods for efficiently measuring growth and physiological responses under field conditions.

3.3 Materials and methods

3.3.1 Location and plant material

The experiment was setup in 2016 in a polytunnel located at the Teagasc Research Centre, Kinsealy Dublin. The polytunnel was a triple-span construction, covered with a white opaque polythene roof (720-gauge (180 micron) UV treated polythene allowing 95% light transmission), and fitted with fixed mesh side ventilation.

During the period of study from March 2016 to March 2017 the mean outside temperature ranged from minimum of -4.8˚C to a maximum of 26.3˚C at the Met Eireann meteorological station at Dublin Airport (4 km from the research site). Temperature in the polytunnel was measured using three mini temperature sensor data loggers (Elitech RC-4; Jingchuang Electric Co., Ltd, Jiangsu, China) which were placed at either end of the experimental area and the third one about midway between these points. The temperature sensors were placed at 1.25 m above ground level. Temperatures were recorded inside the polytunnel from March 2016 to March 2017 and ranged from minimum -2.2˚C to maximum 36.6˚C, with a mean of 9.6˚C. Temperatures could not be controlled in the polytunnel. The mesh sides allowed air to circulate naturally, but ventilation rates could not be controlled.

Seedlings of each species were sourced from different nurseries (Table 3-1). *A. cordata* and *P. sitchensis* were bare-rooted plants and *E. nitens* were plug-grown plants.

Table 3-1: Description of plants used in the experimental setup.

Binomial name	Common name	Seed origin	Provenance code	Plant description†	Plant source	Height at planting (m)	
Eucalyptus nitens	Shining gum	New Zealand	EI-NZ-M56	1-year old plugs (P+1)	Irish plant propagators Ltd.	Min Max Mean	0.31 0.40 0.36
Alnus cordata	Italian alder	United Kingdom	AL-UK403-M55	2-year-old seedlings (2+0) bare roots	None-So-Hardy Ltd	Min Max Mean	0.63 0.77 0.68
Picea sitchensis	Sitka spruce (Oregon)	America	OECD-06639-40	3-year-old transplant (2+1)	Coillte	Min Max Mean	0.45 0.62 0.55

† Plug plants (P) are seedlings grown in individual cells and transplanted with roots already bound in a plug of medium.
2+0 seedlings were grown for 2 year in a seed bed and were undercut
2+1 seedlings were grown for 2 years in a seed bed and 1 more year in a transplant bed

Rigid pots of 35-L capacity were filled with Bord na Móna standard nursery grade 100% peat compost with Osmocote slow release fertilizer @4.5kg m^{-3} incorporated. Each pot had a surface area of 0.126 m^2. All pots were planted on 9th and 10th March 2016. The plants were graded into three size categories (small, medium and large) for potting, with an equal number from each category being allocated to each treatment. In addition, the plants were allocated sequentially in order (small, medium and large) to the pots in an effort to minimise the chance that similarly sized plants would be grouped (both within and between pots).

Pots were irrigated daily using a controlled overhead drip irrigation system (Hunter XC irrigation unit; Hunter Industries, California, USA). Soil moisture was tested twice weekly within each pot using a moisture meter (Delta T; Delta-T Devices Ltd, Cambridge, UK) with a wet sensor probe which converted the output into soil water content (%). Soil water content was maintained above 45% in all pots, through altering the timing and duration of irrigation. This target level ensured that all plants were kept turgid without stress from under or over watering.

3.3.2 Study design and plot layout

The experiment was laid out as a randomised block design (Appendix A) with three planting density treatments repeated nine times for each species. The three treatments comprised low, medium and high-density planting, defined as 1) a pot with one tree planted in the centre, 2) a pot planted with four trees, one of which was in the centre and 3) a pot planted with eight trees, one of which was in the centre, respectively. The centre plant in each pot was the subject of most measurements. Three pots (or plots) from each treatment (nine pots) were arranged in one row (block). The pots were placed in a randomised block design by species. Each species was separated with a buffer zone of pots, which were planted with spare plants, at the top and bottom of each row. However, there was no buffer either side of the rows (Appendix A), due to space restrictions in the polytunnel. The species were not randomised because of the large differences in size between them which might otherwise have confounded the results (i.e. shading effect from adjacent pots with larger trees from other species) (Figure 3-1).

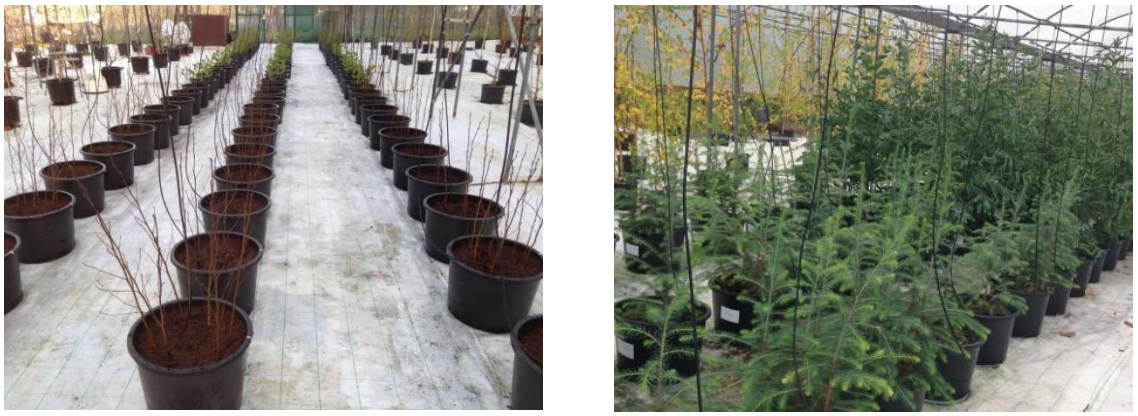

Figure 3-1: The experimental layout at time of planting during March 2016 (left) and in October 2016 after 7 months growth.

Measurements and observations

3.3.2.1 Selection of measurement leaves

Plant tissue maturity can affect sizes of leaves and branches etc. as well as their physiological functioning. Therefore, an index was used to identify leaves of similar maturity for measurement. This was based on a leaf's position from the stem or branch apex, i.e. a leaf plastochron index (LPI) (Chapter 2.3.8). Separate measurements of photosynthesis, chlorophyll concentration, leaf area, leaf dry weight and stomata count were taken on sun and shade leaves. A preliminary study of leaves from various crown positions, using photosynthetic activity light response curves (LRC), was used to determine the location of sun and shade leaves in the crown. The results of the study revealed that shade leaves were found from the 8th and 10th branch down from the apex in *E. nitens* and *A. cordata,* respectively. LRCs were also obtained from fully expanded leaves along the entire branch tip to main stem[2]. This identified the position of the leaf on the branch where shading began. This procedure was used to select the measurement leaves (Table 3-2). LRC was not carried out on *P. sitchensis* as branch material was easily damaged by handling at this young age.

Throughout the text the term "crown" is used to refer to the stem, branch and leaf of a single tree and "canopy" is used to refer to the collective crown structure of all tree(s) in a pot (plot). The term "canopy position" is used to describe the measurement of sun and shade leaves.

[2] The first two leaves on a branch usually had not fully expanded at the time (immature) so measurements were taken from the third leaf.

Table 3-2: Measurements of photosynthetic activity, chlorophyll concentration and specific area were carried out throughout the growing season on leaves of similar developmental stage. A consistent location for measurement was indicated using a plastochron index. Branches (B) were counted from the top of a tree. Leaves (L) were counted from the branch/stem growing tip. In *P. sitchensis* whorl branches were selected.

	Crown position	***Photosynthesis***	***Chlorophyll concentration***	***Specific leaf area***
E. nitens	Sun	L03	L03	L03
	Shade	B08-L08	B08-L08	B08-L08
A. cordata	Sun	B01-L04	B01-L03	B01-L05
	Shade	B10-L05	B10-L05	B11-L06
P. sitchensis	Sun	1st whorl	1st whorl	1st whorl
	Shade	2nd lowest whorl branch	2nd lowest whorl branch	2nd lowest whorl branch

3.3.3 Physiological measurements

Photosynthesis measurements were not assessed for *P. sitchensis* in this experiment. The branches of *P. sitchensis* were so small that growing shoots might have been damaged during the process of measurement.

3.3.3.1 Chlorophyll concentration

Chlorophyll concentration (mg m^{-2}) was evaluated with a chlorophyll concentration meter (Opti-Sciences® CCM-300; Opti-Sciences Inc., NH, USA). The CCM-300 compares chlorophyll fluorescence emission ratio of red 700 nm and far-red 735 nm to chlorophyll content in the range 41 mg m^{-2} to 675 mg m^{-2}. Chlorophyll measurements were taken on 5th and 9th August 2016, on one sun and one shade leaf (Section 3.3.2.1) in all plants of the three species. Five measurements were taken on the adaxial surface of the leaves near the centre of the leaf lamina, avoiding the margins and midrib, (*A. cordata* and *E. nitens*) and on the central adaxial surface of needles (*P. sitchensis*).

3.3.3.2 Photosynthesis measurements

Photosynthesis gas exchange measurements were performed using a portable photosynthesis system (*Li-Cor LI-6400XT; Li-Cor Biosciences; Lincoln, NE*) with an LED light source (*Li-Cor LI-6400-02*) during June and July of 2016 on *A. cordata* and *E. nitens*. Measurements were taken of photosynthetic photon flux density (PPFD) at selected photosynthetic active radiation (PAR) levels and photosynthetic light response

curves (LRC) (P_N/I) were constructed for sun and shade leaves (Section 3.3.2.1). Separate measurements were made at three PAR levels across treatments on *E. nitens* and *A. cordata.*

The LiCor chamber temperature was set to 20 ºC, the mean temperature in the polytunnel during the week prior to gas analysis. There are two infra-red gas analysers (IRGAs) in the LI-6400 referred to as (sample and reference). H_2O was controlled in the sample-IRGA using mole fraction and CO_2 at 403 µmol mol^{-1} was controlled in the reference-IRGA. CO_2 concentration from atmospheric levels measured at Mace Head in Ireland was estimated to be 402.7-403.4 ppm in 2016 according to the World Meteorological Organisation. Stomatal ratio input was calculated as described above (Section 3.3.2.1).

The moisture content of the potting medium was assessed during photosynthesis measurements to ensure that there was no potential effect of water availability on photosynthesis rates. Five moisture readings were taken in the potting medium at evenly spaced arbitrary positions around the pot and the mean calculated. Moisture was maintained above 45% in each pot.

3.3.3.2.1 Light response curves

The response of photosynthesis rate (P_N) to different light intensities was examined through constructing LRCs. A total of 36 LRCs (2 species × 2 canopy positions (sun and shade) x 3 planting densities × 3 blocks) were calculated. Due to the time-demanding nature of the work it was not practical to repeat the measurements. The settings used with the LI-6400 for LRC measurements were: 11 light intensities (0, 25, 50, 100, 250, 500, 800, 1000, 1250, 1500, 2000 µmol (photon) m^{-2} s^{-1}); a wait period of 120s minimum to 200s maximum; IRGA "matching" occurred if elapsed time was >30 minutes; the CO_2 change was 100 ppm; the difference in IRGA's CO_2 was 5 ppm, leaf fan was fixed at maximum (5).

The model used for constructing *LRCs* was the rectangular hyperbola equation based on Michaelis-Menten models (Baly, 1935) and computed using the Microsoft Excel solver tool as described by Lobo et al. (2013). The equation that best fit the data was:

$$P_N = \left[I \times P_{gmax}/\left(I + I_{(50)}\right)\right] - R_D \quad \text{(Eq. 1)}$$

where P_N = net photosynthesis rate [mmol (CO_2) m^{-2} s^{-1}], P_{gmax} = maximum gross photosynthesis rate [mmol (CO_2) m^{-2} s^{-1}], I = photosynthetic photon flux density [mmol (photons) m^{-2} s^{-1}], $I_{(50)}$ = light saturation point [mmol (photons) m^{-2} s^{-1}] at $P_N + R_D = 0.5P_{gmax}$ and R_D = dark respiration rate [mmol (CO_2) m^{-2} s^{-1}] (Kaipiainen, 2009).

The following data were obtained using the model: (i) I_{max} - the light saturation point beyond which there is no significant change in net photosynthesis rate (P_N); (ii) $P_N I_{max}$ – the maximum net photosynthetic rate obtained at Imax; (iii) LCP - the light compensation point, the x-intercept of the light response curve where net photosynthesis is zero, i.e. rate of photosynthesis matches rate of respiration; and (iv) R_D – the dark respiration rate is the respiration regardless of light.

3.3.3.2.2 Photosynthesis measurements at selected PAR levels

The LRC data were used to identify specific PAR levels that were expected to elicit different responses to treatment. Photosynthetic measurements were made of one sun and one shade leaf in all *A. cordata* and *E. nitens* measurement trees (the centre plant × 54 pots). The Li-6400 was set to measure PAR levels of 500, 1,000 and 1,500 µmol m^{-2} s^{-1} with the air flow rate at 500 mml for speed of measurement.

3.3.4 Morphological measurements

Tree height and root collar diameter (RCD) of all plants were measured six days after planting. Thereafter, only the central plant was assessed until the end of the experiment in February 2017 when all plants were measured again. Height was measured every seven days and RCD every 4 weeks. Height was measured from soil surface to plant tip; RCD was measured 5 cm above the surface of the planting medium. The RCD position on the stem was marked to facilitate repeated measurements.

Branch length was measured in February 2017 prior to the end of the experiment. The lengths of the longest branches in the four cardinal directions were obtained. A mean of the four branches was calculated. Live branches were defined as

those which on visual inspection (after mildly "scraping" the bark) had some green chlorophyll and when there was evidence of sap present. Live branches were counted after planting and live and dead branches were determined at the end of the experiment.

3.3.4.1 Leaf measurements

Leaf area and dry weight (*DW*) were measured during October 2016 on two leaves per broadleaved plant and 10 needles per spruce plant (i.e. three treatments × nine pots × three species). All leaves and needles were scanned on a flatbed scanner (DCP-770CW; Brother Industries Ltd.). Leaf surface area was calculated using Easy Leaf Area software (Easlon and Bloom, 2014). Leaves were dried at 70˚C until a steady dry weight was obtained using a balance (Ohaus Pioneer; Ohaus Corporation, New Jersey, USA). Specific leaf area (*SLA*) was calculated using the equation:

$$SLA = leaf\ area\ (cm^2)/dry\ mass\ (g) \quad \text{(Eq. 2)}$$

3.3.4.2 Light interception and leaf area index

Light interception per pot was measured during October 2016 using a single point quantum sensor (LI-190R Li-Cor Biosciences; Lincoln, NE, USA) and a 1-m line quantum sensor (LiCor LI-191R) attached to a data logger (LiCor LI-1400). Quantum sensors measure photosynthetic photon flux density (*PPFD*) in the 400 to 700 nm waveband (expressed as µmol s^{-1} m^{-2}). Before measurements were undertaken, both sensors were operated side-by-side in full light to determine if the readings were comparable. An operating difference of ± 6.7% was obtained.

The line quantum sensor was placed below the crown of each measurement tree and oriented in four cardinal directions around the stem of the central plant in each pot. The single-point quantum sensor recorded the ambient light above the canopy in the polytunnel at the same time as the line-sensor reading. Each pot was removed temporarily from its position and placed in open space in the polytunnel during measurements to ensure that shading from other adjacent pots did not affect the readings.

Leaf area index (*LAI*) was calculated indirectly using the above- and below-canopy light measurements according to the Beer-Lambert Law (Monsi and Saeki, 2005):

$$Beer - Lambert\ law\ l_z/l_0 = exp^{(-k)(LAI)} \quad \text{(Eq. 3)}$$

$$LAI = \log(l_z/l_0)\,/(-0.5) \quad \text{(Eq. 4)}$$

where l_z is the radiation intensity (µmol s^{-1} m^{-2}) measured below the canopy, l_0 the radiation intensity above the canopy, $-k$ the empirical light extinction coefficient (assumed to be 0.5). *LAI* is dimensionless which ranges from 0 (bare ground, no leaf cover) to over 10 (dense forest below-canopy).

3.3.4.3 Stomatal ratio

Stomatal numbers were assessed in September 2016. A clear nail varnish impression of the epidermis was obtained of the abaxial and adaxial surface of two sun leaves and two shade leaves of each species. Clear tape was then used to remove the varnish impression, which was mounted on a slide for analysis (Sampson, 1961). Stomatal density was determined from the number of stoma per field of view with a magnification of 400× and a field of view of 0.126 mm^2 (Figure 3-2). The mean of five separate fields of view per slide were calculated. Photographs of each field of view were obtained using a camera (UEye, IDS-imaging, Germany) attached to a microscope, which had photographic imaging software (Quick Photo Micro 2.3, Promicra, s.r.o. Prague, Czech Republic).

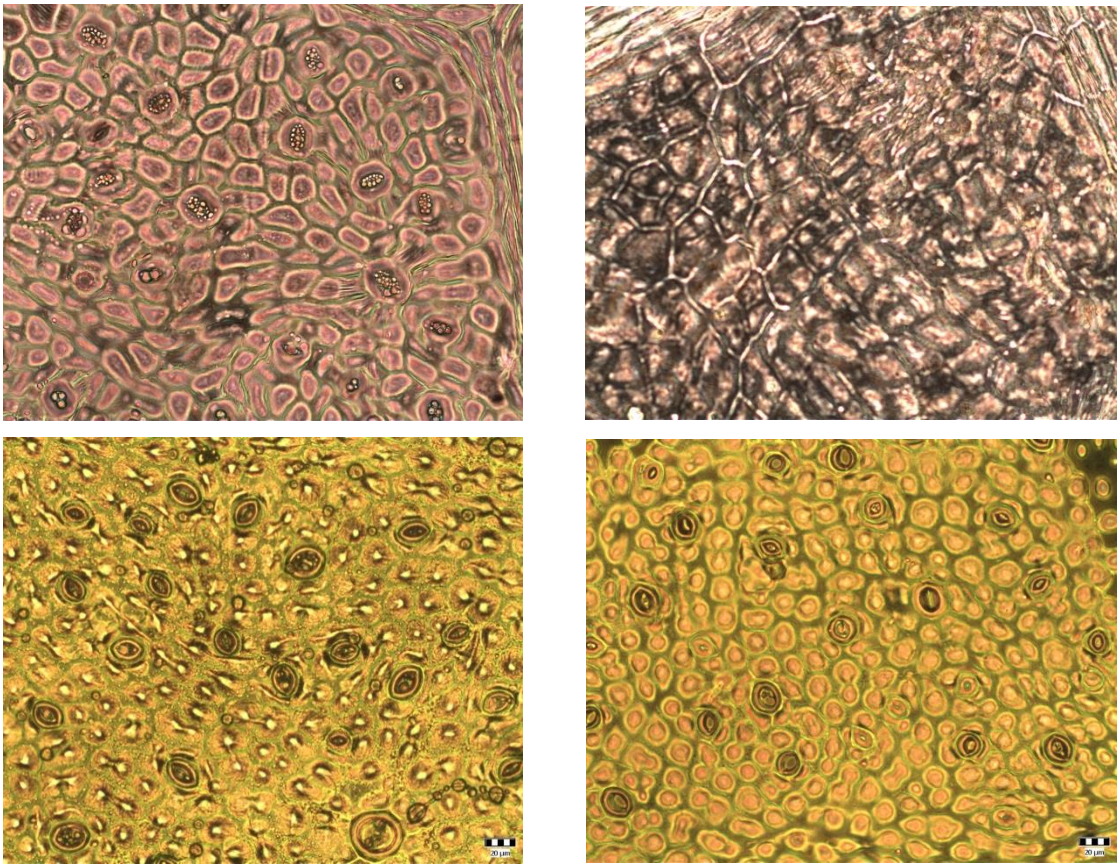

Figure 3-2: Impressions of stomata on leaf surfaces were assessed with imaging software for *A. cordata* on abaxial surface (upper left) and adaxial surface (upper right) and for *E. nitens* abaxial surface (lower left) and adaxial surface (lower right).

3.3.5 Biomass assessments

All measurement trees were harvested, and their component dry biomass determined at the end of the experiment in February 2017. Tree height and RCD were measured prior to harvesting. Branches were cut from the stem and number of 1st order branches and longest branch length were recorded. Roots of the measurement tree were separated from those of neighbouring trees (in the pots containing more than one plant) and washed. Tree biomass was divided into stem, branch, foliage and root components. Foliage of *E. nitens* and *P. sitchensis* were separated from branches. *A. cordata* had shed its leaves prior to assessment.

All components were oven dried at 70°C until constant dry weight (Proe et al., 2002). To obtain a branch to needle ratio for *P. sitchensis,* the dried branches were stripped of needles and weighed separately.

3.3.6 Data analysis

All data was checked for normality. An analysis of variance (ANOVA) using Proc Glimmix with SAS® software (SAS statistical analysis software 9.4; SAS Institute, Cary, NC, USA, 1988) was used to test for the effects of block, planting density and where applicable crown position on growth characteristics such as height, diameter, chlorophyll concentration and photosynthetic activity. A significance level of $P < 0.05$ was applied. An analysis of variance (ANOVA) using Proc Glimmix with SAS® software was used to test for effects of block, planting density and canopy position on I_{max}, $P_N I_{max}$, LCP and R_D.

3.4 Results

With few exceptions, plant growth was reduced as planting density increased. Planting density influenced stem height, root collar diameter (RCD), branch length, branch number, chlorophyll concentration (Ch_{leaf}) and rate of photosynthesis (P_N), as described in detail below.

3.4.1 Photosynthetic activity

3.4.1.1 Chlorophyll concentration

Chlorophyll concentration (Ch_{leaf}) in sun leaves was not affected by planting densities in all three species (Figure 3-3). Ch_{leaf} was significantly lower in sun leaves (277.7 mg m^{-2}) than in shade leaves (313.3 mg m^{-2}) at the low planting density in *A. cordata.* Ch_{leaf} decreased significantly in shade leaves as planting increased from low to high density in *A. cordata* (p = 0.0115) and *E. nitens* (p <0.0001). *P. sitchensis* needles contained the highest concentrations of chlorophyll of the three species (max 515.2 mg m^{-2}, mean 398.3 mg m^{-2}) at low density planting. However, this decreased significantly as planting density increased (Table 3-3).

Table 3-3: Summary ANOVA of the effects of three planting densities (1, 4 and 8 plants per pot) and of the crown position (sun and shade leaves) on leaf chlorophyll concentration in *E. nitens*, *A. cordata* and *P. sitchensis* under polytunnel conditions.Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
	df	F	p	F	p	F	p
Planting density	2	15.3	**<.0001**	5.2	**0.0097**	5.1	**0.0105**
Crown position	1	2.5	0.1251	14.3	**0.0005**	0.2	0.6248
Planting density x Crown position	2	15.6	**<.0001**	2.5	0.0919	0.3	0.7499

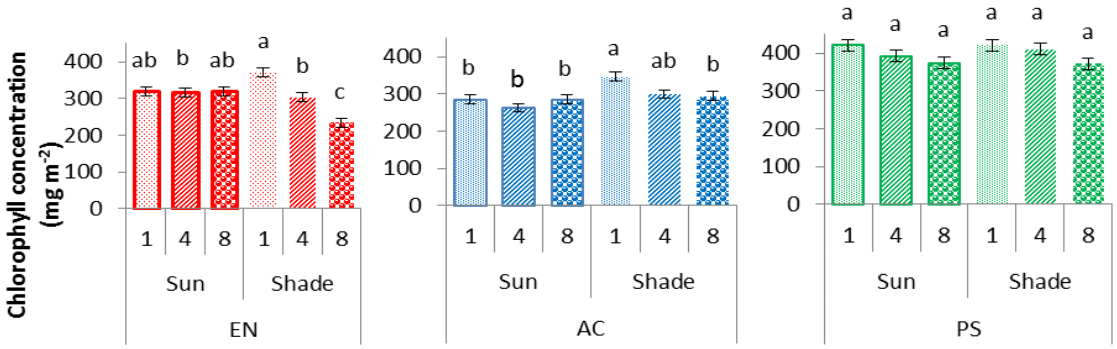

Figure 3-3: Mean chlorophyll concentration in sun or shade leaves at three planting densities (1 to 4 and 8 plants per pot) for *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS).Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments and crown position within species.

3.4.1.2 CO_2 light response

The P_N light response differed between species and crown position (sun vs. shade leaf; Section 3.3.2.1) and declined with planting density (Figure 3-4). Density effects started to become apparent at 50 to 100 µmol m^{-2} s^{-1} PAR in *E. nitens* and between 10 and 50 µmol m^{-2} s^{-1} PAR in *A. cordata* (Figure 3-4).

The light response curves (LRCs) indicated that the photosynthesis rates at maximum irradiance (P_NI_{max}) declined with increasing planting density in *A. cordata,* but not in *E. nitens* (Table 3-4). The light saturation point (I_{max}) declined in *E. nitens* but not in *A. cordata* as planting density increased. Planting density did not affect dark respiration (R_d) and light compensation point (LCP) in either species. The LCP of shade leaves ranged from 9 to 12 µmol m^{-2} s^{-1} for *A. cordata* and 13 to 21 µmol m^{-2} s^{-1} for *E. nitens*.

P_NI_{max} was significantly higher in shade leaves than in sun leaves, and R_D and LCP were significantly higher in sun leaves, but crown position did not affect I_{max} in *E. nitens* (Table 3-4). P_NI_{max} and I_{max} were higher in sun leaves than in shade leaves in *A. cordata,* although there was no impact on R_D and LCP with crown position.

As planting density increased, there was a significant decrease in LRC photosynthesis rate between PAR 500 and 1,000 µmol m^{-2} s^{-1} in *A. cordata* between 500 and 1,500 µmol m^{-2} s^{-1} in *E. nitens*. For this reason, a further evaluation of treatment effects using larger sample sizes at irradiance levels of 500, 1,000 and 1,500 µmol m^{-2} s^{-1} were carried out, as reported below (3.4.1.3).

Table 3-4: A summary ANOVA of the effects of three planting densities (1, 4 and 8 plants per pot) and crown position (sun vs. shade leaves) on photosynthesis rates over eleven irradiance values which formed light response curves from which photosynthesis rates at maximum irradiance ($P_N I_{max}$), light saturation point (I_{max}), dark respiration rate (R_d) and light compensation point (LCP) were obtained for *E. nitens* and *A. cordata*. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*			*A. cordata*		
		df	**F**	**P**	**df**	**F**	**p**
P_NImax	Planting density (PD)	2	3.7	0.1239	2	7.1	**0.0480**
	Crown position (CP)	1	9.2	**0.0229**	1	17.9	**0.0083**
	CP × PD	2	0.1	0.9142	2	0.9	0.4651
Imax	PD	2	9.2	**0.0319**	2	5.3	0.0762
	CP	1	1.2	0.3221	1	18.4	**0.0078**
	CP × PD	2	0.3	0.7559	2	0.2	0.8124
R_D	PD	2	0.6	0.6128	2	0.0	0.9836
	CP	1	7.0	**0.0388**	1	0.0	0.9545
	CP × PD	2	0.3	0.7879	2	0.5	0.6165
LCP	PD	2	1.6	0.3178	2	0.0	0.9984
	CP	1	15.8	**0.0073**	1	4.4	0.0911
	CP × PD	2	0.4	0.7199	2	0.8	0.5088

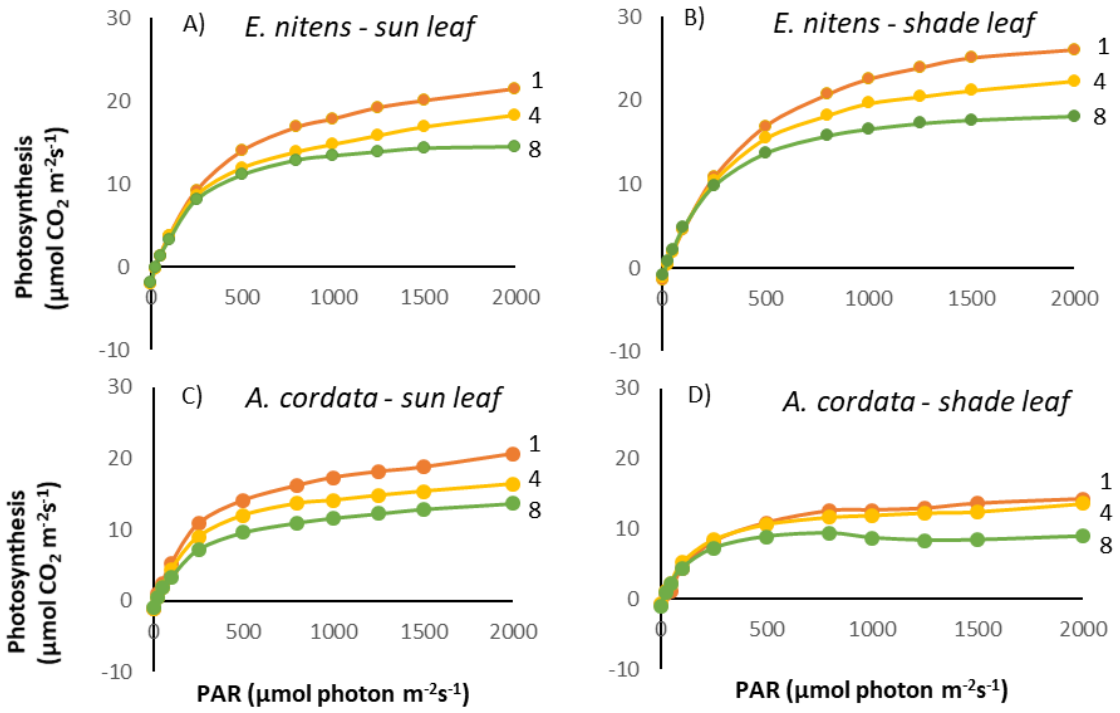

Figure 3-4: Light response curves for sun and shade leaves *E. nitens* (A, B) and *A. cordata* (C, D) at three planting densities (1, 4 and 8 plants per pot).

3.4.1.3 Fixed light level responses

Planting density and crown position (sun vs. shade leaf, section 3.3.2.1) influenced photosynthesis (CO_2) and transpiration (H_20) rates in *E. nitens and A. cordata* at 500, 1,000 and 1,500 PAR (Table 3-5, Table 3-6). Photosynthesis rates were significantly higher in sun leaves than in shade leaves of both species (Table 3-5).

Planting density did not affect P_N in sun leaves but there was a significant decrease in P_N in shade leaves measured at 500 and 1,000 µmol m^{-2} s^{-1} PAR as density increased in *E. nitens* (Figure 3-5, Table 3-5). However, planting density effects were not apparent at PAR of 1,500 µmol m^{-2} s^{-1} in *E. nitens*. There was also a significant increase in P_N (sun leaves) as PAR increased from 500 to 1,000 and 1,500 µmol m^{-2} s^{-1} in *E. nitens* (Table 3-5). The highest P_N was found in *E. nitens* sun leaves at PAR of 1,500 µmol m^{-2} s^{-1}.

Planting density did not affect P_N in the sun leaves in *A. cordata* at 500, 1,000 or 1,500 µmol m^{-2} s^{-1} PAR (Figure 3-5). However, shade leaf P_N declined as planting density increased at 500, 1,000 and 1,500 µmol m^{-2} s^{-1} PAR.

Transpiration rates declined significantly at PAR 500 µmol m^{-2} s^{-1}, from sun to shade leaves at all planting densities and at PAR 1,500 µmol m^{-2} s^{-1} at high planting density (Figure 3-6). The transpiration rate in sun or shade leaves at 1,000 µmol m^{-2} s^{-1} PAR was not influenced by either its position in the crown or planting density in *E. nitens*. Transpiration rates were significantly lower in shade than in sun leaves in *A. cordata* at all three PAR levels (Table 3-6). However, planting density did not influence transpiration rates in *A. cordata.*

Table 3-5: ANOVA of the effects on photosynthesis rates in response to three planting densities at 500, 1,000 and 1,500 µmol m^{-2} s^{-1} PAR and with crown position (sun or shade leaves) for *E. nitens* and *A. cordata*. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*	
	df	F	p	F	p
Planting density (PD)	2	5.7	**0.0132**	6.8	**0.0074**
Crown position (CP)	1	591.2	**<.0001**	131.2	**<.0001**
PAR	2	33.8	**<.0001**	42.7	**<.0001**
PD x CP	2	1.0	0.3689	7.5	**0.0029**
PD x PAR	4	0.6	0.6542	0.8	0.5574
CP x PAR	2	29.1	**<.0001**	7.6	**0.0014**
PD x CP x PAR	4	0.2	0.9310	0.6	0.6569

Table 3-6: ANOVA of the effects on photosynthesis rates and transpiration rates on *E. nitens* and *A. cordata* at 500, 1,000 and 1,500 µmol m^{-2} s^{-1} PAR at three planting densities (1, 4 and 8 plants per pot), crown position (sun vs. shade leaves) and crown position × planting density.Values in bold indicate significance at p ≤0.05.

Source of variation			*E. nitens*		*A. cordata*	
		df	F	p	F	p
Photosynthesis (CO_2) rates						
PAR 500 µmol m^{-2} s^{-1}	Planting density (PD)	2	4.1	**0.0242**	2.9	0.0644
	Crown position (CP)	1	67.2	**<.0001**	29.5	**<.0001**
	CP × PD	2	0.6	0.7833	3.8	**0.0322**
PAR 1,000 µmol m^{-2} s^{-1}	PD	2	9.4	**0.0005**	3.4	**0.0424**
	CP	1	362.6	**<.0001**	28.2	**<.0001**
	CP × PD	2	0.7	0.4921	2.8	0.0747
PAR 1,500 µmol m^{-2} s^{-1}	PD	2	4.1	**0.0246**	7.1	**0.0024**
	CP	1	183.2	**<.0001**	63.3	**<.0001**
	CP × PD	2	0.4	0.7015	1.6	0.2150
Transpiration (H_2O) rates						
PAR 500 mmol H_2O m^{-2} s^{-1}	PD	2	2.8	0.0713	2.4	0.0997
	CP	1	68.7	**<.0001**	175.8	**<.0001**
	CP × PD	2	0.1	0.8990	0.1	0.9462
PAR 1,000 mmol H_2O m^{-2} s^{-1}	PD	2	3.8	**0.0310**	1.9	0.1686
	CP	1	0.9	0.3435	175.5	**<.0001**
	CP × PD	2	1.2	0.3007	0.5	0.6378
PAR 1,500 mmol H_2O m^{-2} s^{-1}	PD	2	5.1	**0.0107**	1.6	0.2226
	CP	1	18.7	**0.0001**	162.2	**<.0001**
	CP × PD	2	0.9	0.4018	1.2	0.3071

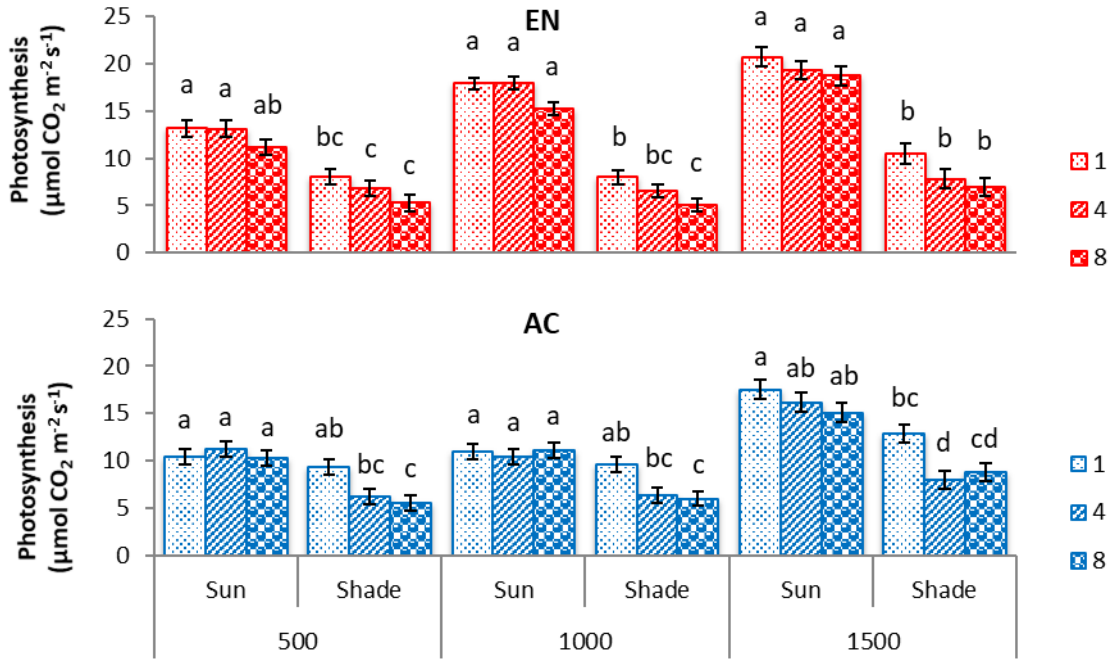

Figure 3-5: Mean photosynthesis rates at irradiance levels of 500, 1,000 and 1,500 µmol m^{-2} s^{-1} in response to crown position (sun and shade leaves) and three planting densities (1, 4 or 8 plants per pot) in *E. nitens* (EN) and *A. cordata* (AC). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) within PAR, within species.

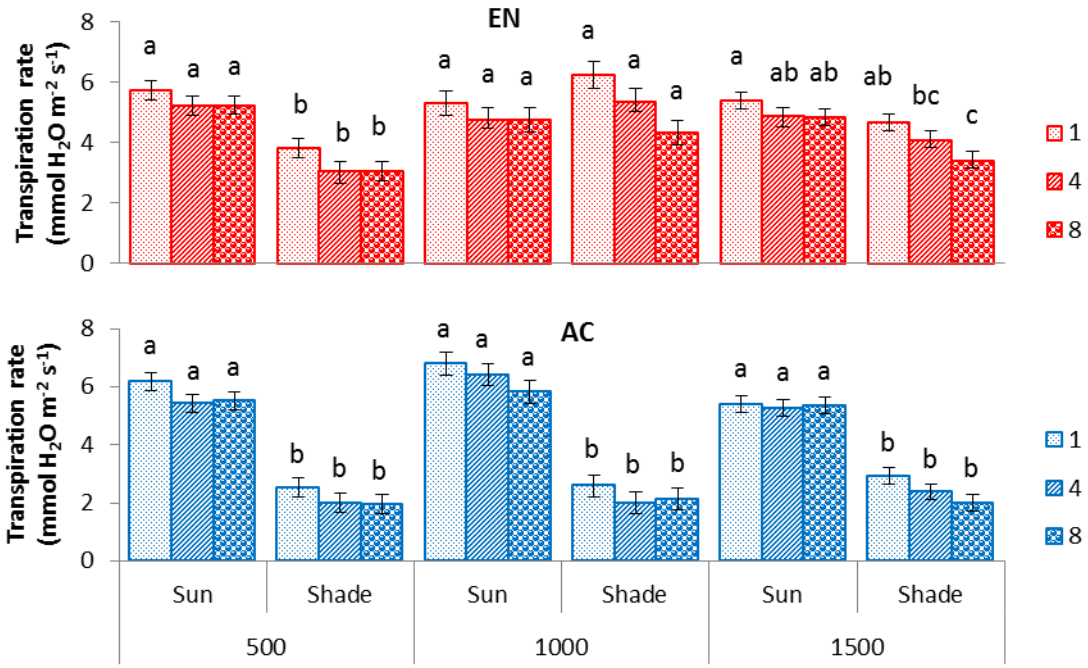

Figure 3-6: Mean transpiration rates at irradiance levels of 500, 1,000 and 1,500 µmol m^{-2} s^{-1} in response to crown position (sun and shade leaves) and three planting densities (1, 4 or 8 plants per pot) in *E. nitens* (EN) and *A. cordata* (AC). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) within PAR, within species.

3.4.1.4 Leaf characteristics

The stomatal ratio (i.e. ratio of stomatal density of adaxial (upper) to abaxial (lower) surfaces) differed between species. *E. nitens* and *P. sitchensis* produce stomata on both leaf surfaces (i.e. amphistomy), and ratios were 0.85 (23/27) and 0.33 (5/16), respectively. *A. cordata* only produces stomata on the abaxial side of the leaves (i.e. hypostomy) with a mean of 159 stomata per mm^2.

The position within the crown (see Section 3.3.2.1) and planting density affected leaf area and dry weight (DW). Shade leaves were significantly heavier and larger in area at low density than at high density planting in *E. nitens.* However, planting density did not affect leaf area and DW of sun leaves (Figure 3-7). The sun and shade leaves of *A. cordata* grown at the lowest planting density had larger mean leaf area and greater mean leaf DW than those grown at higher density in (Table 3-7, Figure 3-7). Leaf area and DW of *P. sitchensis* sun leaves declined significantly from high density to low density planting but planting density did not affect the DW of shade leaves (Figure 3-7).

The specific leaf area of sun and shade leaves was significantly larger at high planting density than at medium and low-density treatments in *A. cordata* (Table 3-8). Planting density did not influence the SLA in *P. sitchensis* or *E. nitens*.

The leaf area index (LAI) increased significantly from low to medium densities in *A. cordata* and *E. nitens*, but there was no difference in LAI between medium and high densities for either species (Table 3-8). The LAI was significantly lower ($p < 0.0001$) in *P. sitchensis* than in *E. nitens* and *A. cordata* at each planting density (Figure 3-8).

Table 3-7: Summary ANOVA of leaf area, dry weight and SLA at three planting densities (1, 4 and 8 plants per pot) for *E. nitens*, *A. cordata* and *P. sitchensis* at the crown positions (sun and shade leaves). Values in bold indicate significance at p ≤0.05.

Source of variation			*E. nitens*		*A. cordata*		*P. sitchensis*	
		df	F	p	F	p	F	p
Leaf area	Sun × Planting density (PD)	2	0.2	0.7953	14.6	**0.0145**	7.6	**0.0437**
	Shade × PD	2	8.1	**0.0394**	9.0	**0.0329**	0.3	0.7606
Dry weight	Sun × PD	2	0.3	0.7771	11.1	**0.0234**	14.3	**0.0150**
	Shade × PD	2	39.5	**0.0023**	34.7	**0.0030**	0.0	0.9642
SLA	Sun × PD	2	0.1	0.9233	21.8	**0.0070**	2.2	0.2311
	Shade × PD	2	0.0	0.9623	20.9	**0.0076**	0.4	0.6709

Table 3-8: A summary of ANOVA of the mean leaf area, mean dry weight and SLA (area/dry weight) for the effect at the crown positions (sun and shade leaves), at three planting densities (1, 4 and 8 plants per pot) and crown position × planting density for *E. nitens*, *A. cordata* and *P. sitchensis*; along with a summary of LAI at three planting densities for the three species. Values in bold indicate significance at p ≤0.05.

Source of variation			*E. nitens*		*A. cordata*		*P. sitchensis*	
		df	F	p	F	p	F	p
Leaf area	Crown position (CP)	1	5.0	0.0660	29.8	**0.0016**	26.7	**0.0021**
	Planting density (PD)	2	0.9	0.4692	18.4	**0.0096**	4.5	0.0954
	CP × PD	2	1.9	0.2241	2.0	0.2226	5.8	**0.0390**
Dry weight	CP	1	0.0	0.9809	24.2	**0.0027**	114.8	**<.0001**
	PD	2	0.6	0.5898	16.6	**0.0116**	5.0	0.0824
	CP × PD	2	2.2	0.1916	1.4	0.3150	34.8	**0.0005**
SLA	CP	1	26.7	**0.0036**	14.4	**0.0091**	0.0	0.8899
	PD	2	0.0	0.9605	29.2	**0.0041**	1.8	0.2798
LAI	PD	2	4.7	**0.0249**	82.7	**<.0001**	3.0	0.0824

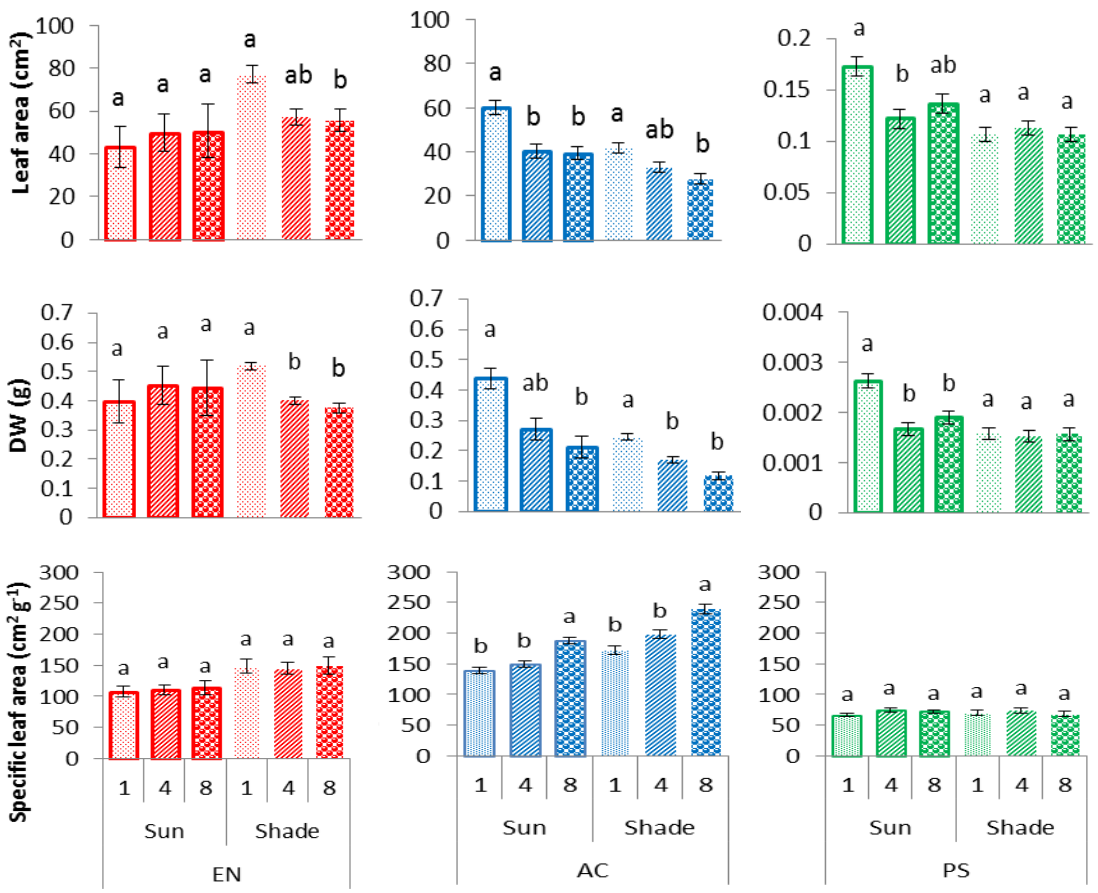

Figure 3-7: Mean leaf area, mean dry weight (DW) and specific leaf area at three planting densities (1, 4 or 8 plants per pot) for *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) at the crown position (sun or shade leaves). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between the treatments within crown position (sun or shade leaves).

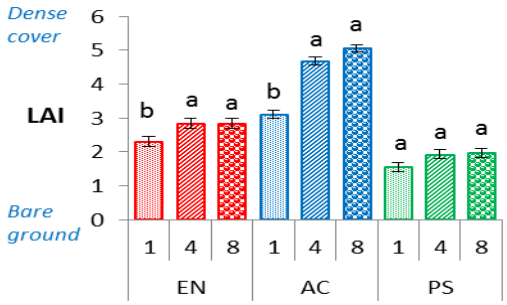

Figure 3-8: Mean leaf area index (LAI) for *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) under polytunnel condition at three planting densities (1, 4 or 8 plants per pot). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within a species.

3.4.2 Morphology

Tree height and root collar diameter increment (RCD) were significantly lower ($p < 0.0005$) at the higher than the low planting density in *E. nitens* and *A. cordata* (Table 3-9). However, although RCD increment of *P. sitchensis* was also lower at higher densities, there was no significant impact on height increment (Figure 3-10).

Branch length in all species was greatest at low planting density and decreased significantly as planting density increased (Figure 3-9). Branchiness (number of live branches per tree) significantly decreased from the low to the high planting density treatment in *E. nitens* (low density = 30 branches, high density = 18 branches) and *A. cordata* (low density = 35 branches, high density = 25 branches) (Figure 3-10). There was no treatment effect on the number of live branches in *P. sitchensis*. There were significantly higher numbers of dead branches on *E. nitens* trees as planting density increased from low to medium density (Figure 3-10).

Mean stem volume per tree differed significantly between species (Figure 3-11). The largest stem volume was produced in *A. cordata* followed by *E. nitens* with *P. sitchensis* trees having the smallest volume. Mean stem volume declined as planting density increased in *A. cordata*. Planting density also affected mean stem volume in *E. nitens,* which declined as planting increased from low to medium density. Mean stem volume declined as density increased from medium to high density in *P. sitchensis*.

Mean height increased as planting density increased in *E. nitens*, resulting in taller and thinner crowns which led to a significant increase in stem height: branch

length ratio (Figure 3-11). Stem height: branch length ratio increased from the low to medium density treatment in *A. cordata* and *P. sitchensis*. Crown volume declined from the low to the medium densities in all species, although there was no further increase at the high density (Figure 3-11).

Table 3-9: Summary ANOVA of the impact of three planting densities (1, 4 and 8 plants per pot) on a series of growth related traits for *E. nitens*, *A. cordata* and *P. sitchensis*. Values in bold indicate significance at p ≤0.05 between treatments within a species.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
	df	F	p	F	P	F	p
Stem height	2	5.2	**0.0179**	23.5	**<.0001**	1.6	0.2332
Root collar diameter	2	29.6	**<.0001**	62.0	**<.0001**	38.9	**<.0001**
Branch length	2	38.4	**<.0001**	44.2	**<.0001**	20.9	**<.0001**
Number of branches – live	2	9.3	**0.0021**	15.2	**0.0002**	3.2	0.0699
Number of branches – dead	2	16.6	**<.0001**	-	-	-	-
Stem volume	2	23.0	**<.0001**	46.3	**<.0001**	21.9	**<.0001**
Crown volume	2	30.9	**<.0001**	26.8	**<.0001**	19.8	**<.0001**
Height/branch length ratio	2	15.4	**0.0002**	33.8	**<.0001**	8.17	**0.0036**
Branchiness count/height ratio	2	6.3	**0.0095**	0.3	0.7414	0.7	0.5349

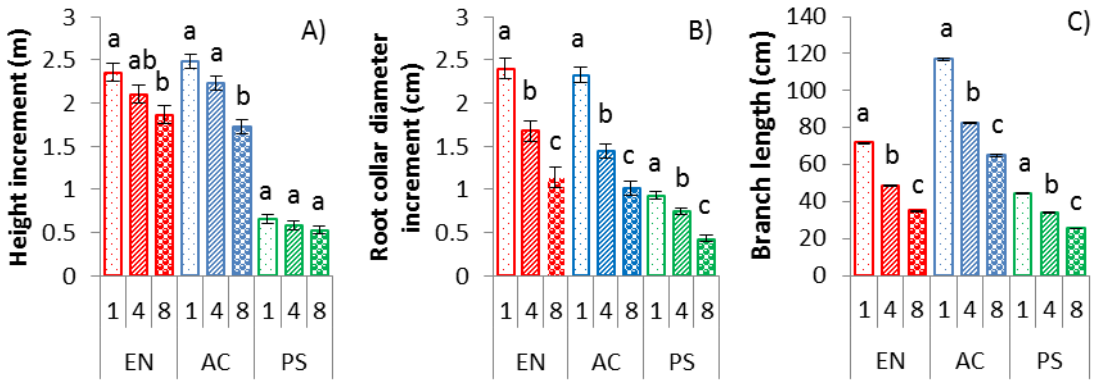

Figure 3-9: Mean height (m) increment, root collar diameter (cm) increment and branch length (cm) of *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) at three planting density (1, 4 and 8 plants per pot). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within a species.

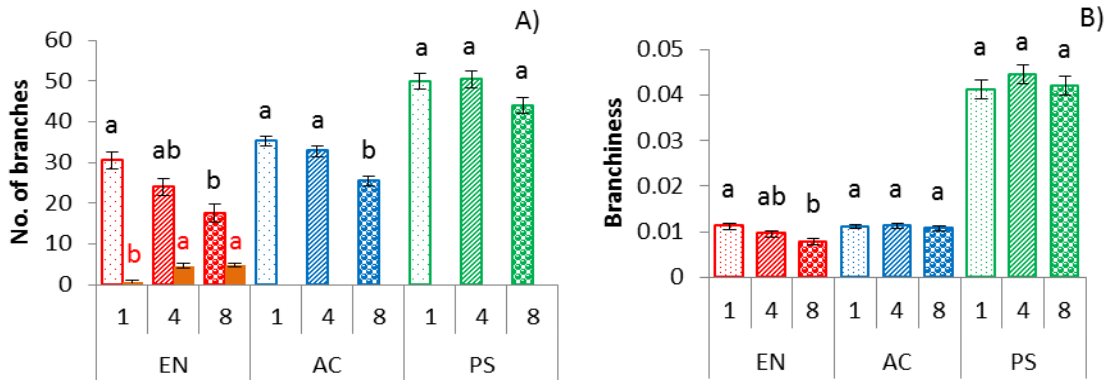

Figure 3-10: (A) Mean number of branches – live [hatched colour (EN, AC and PS)] with dead number of branches – [solid colour (EN)], and (B) branchiness (number of branches to height ratio) of *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) at three planting density (1 to 4 and 8 plants per pot). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within a species.

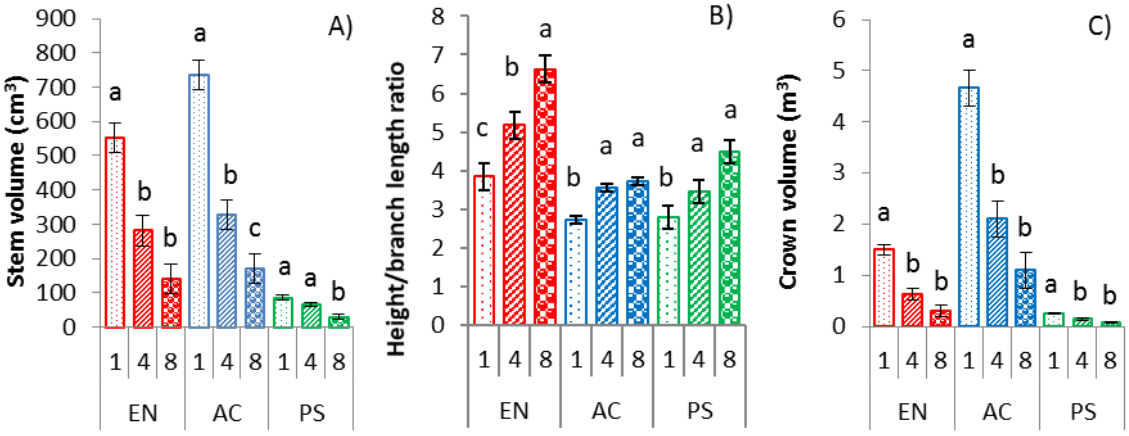

Figure 3-11: Mean (A) stem volume, (B) height to branch length ratio and (C) crown volume with *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) at three planting densities (1 to 4 and 8 plants per pot). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within a species.

3.4.3 End-of-season biomass

Planting density influenced all biomass components in all species after 10 months growth in the polytunnel (Table 3-10). Stem, branch and root biomass per tree was significantly higher in trees grown at the low compared with the medium planting density in *E. nitens*, with no difference between medium and high planting density. Stem, branch and root biomass declined significantly as planting density increased in *P. sitchensis* (Figure 3-12). The amount of biomass for all above ground plant components was significantly lower in *P. sitchensis* compared to the broadleaved species. Stem biomass declined significantly as planting density increased in

A. cordata. Root and branch biomass were significantly greater in the low and medium planting density treatments but there was no further reduction at the highest density.

Biomass components per unit area (centre plant × the number of stems per pot) were greater at the medium density than at the lower density in the three species (Table 3-10). The high-density planting did not result in any further increase. *A. cordata* produced a significantly greater total biomass at all planting densities than either *E. nitens* or *P. sitchensis*.

The percentage of biomass allocated to stem tissue increased in all species as planting density increased, with a corresponding decrease in branch biomass (Figure 3-13). The percentage of root biomass in *E. nitens* and *P. sitchensis* also decreased as planting density increased. Planting density did not affect root biomass in *A. cordata*. A significantly larger proportion of biomass was allocated to roots and branches and a smaller proportion to stems in *P. sitchensis* than in the other two species. Over 50% of the biomass was allocated to stem components at low planting density in *E. nitens,* which increased significantly to 70% as planting density increased, while branch and root biomass decreased. The smallest proportion of biomass was distributed to roots in *E. nitens,* with 80-85% of biomass being allocated to above ground growth.

The root-to-shoot ratio was significantly greater at low than at high planting densities in *E. nitens* and *P. sitchensis* with no decline from low to medium density (Figure 3-13). There was no impact of planting density on root: shoot ratio for *A. cordata.*

Table 3-10: Summary ANOVA of biomass components (stem, branch, leaf and root) in *E. nitens*, *A. cordata* and *P. sitchensis* and all biomass components per unit area (whole plant × stems per pot). Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
	df	F	p	F	p	F	P
Biomass							
Total (not including leaves)	2	29.3	**<.0001**	50.2	**<.0001**	48.1	**<.0001**
Stem	2	14.8	**0.0002**	49.1	**<.0001**	30.9	**<.0001**
Branches	2	49.4	**<.0001**	46.8	**<.0001**	39.2	**<.0001**
Leaves	2	21.2	**<.0001**	-	-	26.6	**<.0001**
Aboveground	2	27.3	**<.0001**	54.3	**<.0001**	43.7	**<.0001**
Belowground	2	25.2	**<.0001**	31.0	**<.0001**	47.9	**<.0001**
Above/Below ground ratio	2	6.0	**0.0114**	1.2	0.3302	7.5	**0.0050**
Biomass per unit area							
Total (not including leaves)	2	4.9	**0.0226**	5.1	**0.0193**	41.7	**<.0001**
Stem	2	6.6	**0.0081**	8.5	**0.0031**	58.4	**<.0001**
Branch	2	2.0	0.1665	1.5	0.2439	22.3	**<.0001**
Leaves	2	3.9	**0.0424**	-	-	22.5	**<.0001**
Aboveground	2	5.8	**0.0127**	6.3	**0.0096**	42.4	**<.0001**
Belowground	2	1.5	0.2571	2.7	0.0985	30.8	**<.0001**

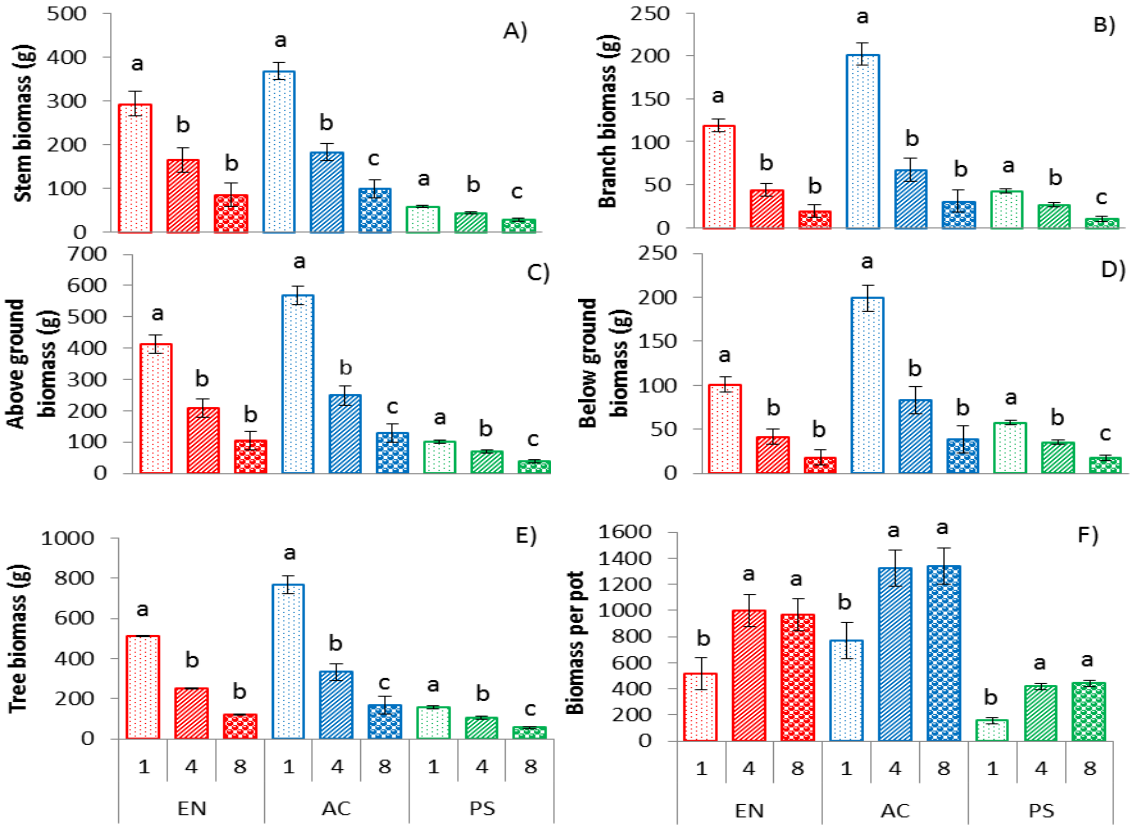

Figure 3-12: Mean A) Stem biomass, B) Branch biomass, C) above-ground biomass (stem and branch only), D) below-ground biomass, E) total tree biomass (above and below ground) and F) biomass per unit area (total tree biomass × stocking) with three planting densities (1, 4 and 8 plants per pot) after 10 months growth of *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within species.

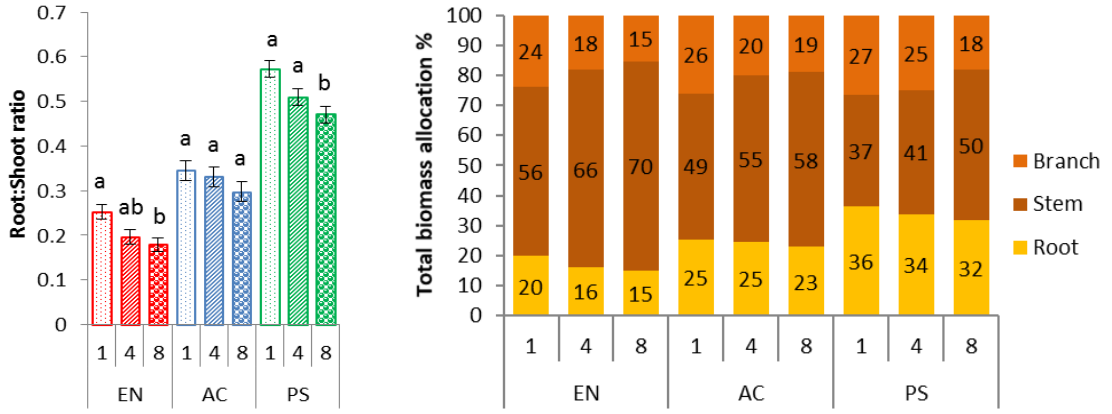

Figure 3-13: Mean root: shoot ratio and total percentage biomass allocated to stem, branch and root with three planting densities (1, 4 and 8 plants per pot) for *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) after 10 months growth. Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p ≤0.05) between treatments within species. Labels indicate percentage of total biomass of each tree component.

3.5 Discussion

The higher planting densities of four and eight plants per pot (surface area 0.126 m^2) used in this study were designed to force competition during the early growth period (<1 year). Although competition caused morphological and physiological changes in all three species, the changes were most pronounced in *A. cordata* and *E. nitens*, with small but significant leaf-level changes in *P. sitchensis*. The impact of planting density on crown development differed with species. Planting density affected photosynthetic rates in sun and shade leaves in *E. nitens* and *A. cordata* and each species differed in their utilisation of irradiance. The effect of planting density on height and diameter growth was observed during the 10 months of growth in *E. nitens* and *A. cordata*. In contrast, planting density did not affect height growth by the end of the study in *P. sitchensis*. Planting density affected tree architecture, altering the amount of biomass allocated between stems, branches and roots in response to competition in the three species studied. Generally plants will allocate more biomass to above-ground components when above-ground competition is stronger and more to roots when competition below-ground is stronger (Poorter et al., 2012). Without exception, as planting density increased a greater proportion of biomass was allocated to the stem, while the amount allocated to branches decreased in all species. The proportion of biomass allocated to roots declined as stocking levels increased in *E. nitens* and *P. sitchensis,* but not in *A. cordata*.

3.5.1 E. nitens

Self-pruning of lower branches had begun in *E. nitens,* with a greater number of dead branches per tree being recorded in the lower crown in response to increasing planting density, compared with *A. cordata* or *P. sitchensis*. This strategy ensured that *E. nitens* maintained a shallow crown with a lower proportion of shade leaves. After only 10 months growth, tree stems were slimmer and crowns shallower with shorter branches in those grown at close than at wide spacing. This demonstrates that *E. nitens* acclimates to the growing conditions very early in growth (<1 year). A similar decline in the allocation of biomass to stems and crowns resulting in response to higher planting

density was identified in *E. nitens* after seven years of growth in the field in Tasmania (Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003).

New branches and leaves were produced higher up in the tree so there was little change in SLA as tree height increased in *E. nitens* in this study. The LAI ranged from 2.3 at the lowest to 2.8 at the highest density in *E. nitens.* These LAI values are low compared to those recorded for other temperate evergreen conifer and broadleaved species, which often range from 5.1-6.7 (Asner et al., 2003). However, the trees were relatively young (8 months old) when the LAI was measured in this study. The LAI results for *E. nitens* suggest that it maintains a more open canopy than most other broadleaved species.

Higher planting densities will cause stress as more plants must compete for fewer resources. Stress tends to cause a reduction in leaf chlorophyll concentration (Ch_{leaf}) in plants prior to leaf abscission (Carter and Knapp, 2001). Shade leaves have a lower Ch_{leaf} (Loach, 1967). The Ch_{leaf} significantly declined in the shade leaves as planting density increased in *E. nitens* in this study. As light levels decline in the shade of the canopy and a leaf fails to maintain a positive carbon balance, chlorophyll is broken down into soluble sugars and is translocated from the dying leaf in advance of abscission (Ördög and Molnár, 2011). Therefore, it would appear that the lower leaves and branches were shed relatively soon after planting in *E. nitens* when compared to the other two species.

There was a significantly lower dark respiration rate (R_D) and light compensation point (LCP) in shade leaves than in sun leaves in *E. nitens*. Shade-tolerant species, such as *Acer rubrum, A. saccharum* and *Fagus grandifolia* have low R_D which results in a low LCP (Loach, 1967), allowing them to maintain higher rates of photosynthesis at lower light intensity than shade-intolerant species. A lower LCP has the advantage of helping to maintain a carbon balance at lower light levels in shade leaves (Boardman, 1977). Light saturation point (I_{max}) is highest in shade tolerant species (Loach, 1967). The I_{max} did not change in the crown in *E. nitens,* suggesting that acclimation to shade occurred after the leaves had fully developed. The low R_D and LCP and higher I_{max} in shade leaves resulted in the photosynthesis rates at maximum irradiance ($P_N I_{max}$) being higher in shade leaves in *E. nitens* in this study. This means

that photosynthesis production probably varied little within the crown of *E. nitens* trees.

E. nitens distributed the least proportion (<20%) of biomass to roots, resulting in a significantly lower root-to-shoot ratio, which decreased as planting density increased. In contrast, the root-to-shoot ratio was not affected by spacing after 10 years growth in *E. camaldulensis* (Barton and Montagu, 2006). *E. nitens* diverted a large proportion of photosynthate to stem biomass as stocking increased in this study, while the proportions allocated to branches and roots declined. Although a greater stem biomass may be a desirable characteristic, a low root-to-shoot ratio could result in lower stability to wind exposure in the field.

3.5.2 A. cordata

A. cordata growth was vigorous over the 10 months of observation, producing a significantly larger crown and stem volume at wider spacing than in the other two species. It also had a relatively lower height to branch ratio than *E. nitens*. Although branch length decreased as density increased in *A. cordata,* branch growth was more vigorous than in the other two species. The LAI ranged from 3.1-5.1 in *A. cordata* and was already within the normal range expected for a broadleaved species (as discussed above).

Shade leaves are often larger and thinner than sun leaves (Taiz and Zeiger, 2010). However, shade leaves were smaller and lighter in *A. cordata* in this study, resulting in a significant increase in SLA as planting density increased. As planting density increased Ch_{leaf} declined, indicating that leaves were affected by shading and possibly also by other stresses. As light penetrates through a tree crown, the photosynthetic photon flux density (*PPFD*) generally declines. Photosynthesis rates declined in shade leaves as planting density increased in *A. cordata*. However, unlike that of *E. nitens,* the branches and leaves were slow to shed in the lower crown of *A. cordata.* Although Ch_{leaf} declined with planting density, indicating the effects of stress, little leaf or branch shedding took place and *A. cordata* maintained a near constant number of branches per unit height at all planting densities.

Planting density or crown position (sun vs. shade leaves) did not affect the R_D or LCP recorded in *A. cordata.* The LCP in *A. cordata* ranged from 9 to 15 µmol m^{-2} s^{-1}. Typical values for the LCP of sun leaves range from 28 to 67 µmol m^{-2} s^{-1}, with values for the shade leaves ranging from 1 to 25 µmol m^{-2} s^{-1} (Heuvel et al., 2004; Lombardini et al., 2009). These values place the sun and shade leaves of *A. cordata* in the shade leaf range, based on the LCP data. Leaves with a lower LCP will be better able to utilise the lower irradiance level available to shade leaves than those with sun leaf characteristics. The values obtained for R_D and LCP in *A. cordata* were lower than in *E. nitens* and would appear to be closer to the typical values expected in a shade tolerant species. The shade leaves also maintained a low I_{max} compared to the sun leaves, which is a characteristic typically associated with shade adaption. The I_{max} reflects the maximum irradiance to which a leaf was exposed to during growth (Taiz and Zeiger, 2010). Overall the $P_N I_{max}$ declined significantly as planting density increased, which would have reduced the productivity potential of shade leaves.

There was no reduction in the proportion of biomass allocated to roots in *A. cordata*, indicating that the roots were not responding to planting density in this study. It was the only species in the study to maintain a similar root-to-shoot ratio as planting density increased. *A. cordata* trees produced the largest crown volume of the three species. This growth strategy proved efficient, as *A. cordata* generated a higher quantity of biomass than either *E. nitens* or *P. sitchensis* during the 10 months of observation.

3.5.3 P. sitchensis

Slow initial height and diameter growth was observed in *P. sitchensis* compared to *E. nitens* and *A. cordata*. However, the number of branches per unit height was over four times greater than that recorded in the other two species and did not change with stocking after 10 months growth in the polytunnel. Slow height growth increment, combined with heavy branching, characterises *P. sitchensis* growth for up to about 6 years (Cochrane and Ford, 1978). The low LAI, which ranged from 1.6-2.0, may also be attributed to the slow initial growth of *P. sitchensis.* The increased stocking level

significantly supressed branch elongation and stem volume production, which resulted in a slimmer crown.

The sun leaves were larger at the low planting density than at high density in *P. sitchensis*, which resulted in a larger photosynthetic surface area and higher production potential at the low density. Shade leaves have a lower Ch_{leaf} than sun leaves in *P. sitchensis* at >10 years old (Lewandowska and Jarvis, 1977). The Ch_{leaf} was similar in the sun and shade leaves of *P. sitchensis* in this study. However, as planting density increased, Ch_{leaf} declined. This demonstrated that the trees at higher density were showing signs of competition stress at leaf level in *P. sitchensis*, but no difference was found between needle position in the crown at this young age.

The proportion of biomass allocated to roots was significantly greater in *P. sitchensis* than the other two species, with almost one third of total biomass being allocated to roots irrespective of the planting density. After three growing seasons there was a significant increase in root-to-shoot ratio in a study of 12 families of *P. sitchensis* in UK (Byers et al., 1997). The total biomass at tree level and per unit area of *P. sitchensis* was the smallest of the three species and tree biomass decreased significantly as planting density increased. This is probably due to the effect of planting density, which resulted in the reduction in the needle size in *P. sitchensis,* possibly reducing productivity potential.

3.6 Conclusions

The three species differed in their response to planting density in this study. Planting density effects were larger in *A. cordata* and *E. nitens* than in *P. sitchensis.* High planting density resulted in a decline in crown size, chlorophyll concentration (shade leaves) and photosynthesis rate (shade leaves) in *E. nitens,* and changes in response to density were larger than those recorded in *A. cordata* and *P. sitchensis*. *E. nitens* also had a significantly larger height to branch ratio than the other species, which increased as planting density increased. The sun leaves in *E. nitens* did not respond to competition, at least based on the physiological responses measured in this study. The small crown volume of *E. nitens* trees resulted in a lower tree biomass than in *A. cordata* at each of the planting densities. The trees of *A. cordata* had larger crowns

and longer branches than in those of *E. nitens* or *P. sitchensis* at all planting densities. Leaf area leaf dry weight and photosynthetic rates declined as planting density increased in sun and shade leaves in *A. cordata*. However, *A. cordata* generated a large crown which resulted in the production of a larger amount of biomass than in either *E. nitens* or *P. sitchensis*. *P. sitchensis* grew slowly, but it had the highest root-to-shoot ratio and had a very dense canopy. The results of this study also indicated that chlorophyll concentration and photosynthesis rates of shade leaves were particularly useful in identifying competition stress in response to higher planting density. Measurements of branch length and crown height were particularly useful in characterising the changes in the tree crown as competition increased.

3.7 References

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4 Early impact of planting density on field growth, and morphological and physiological responses in *Eucalyptus nitens, Alnus cordata* and *Picea sitchensis*

4.1 Abstract

The impact of planting density on the growth and physiological response of three potential short rotation forestry species, shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) were investigated in this study over a four-year period. The three species were planted in a field trial in Co. Wexford. The trial was laid down as a randomised block design containing four planting densities (1,333 – 40,000 stems ha^{-1}) per species. Height, stem diameter, branch length, diameter and quantity, crown height, along with shade leaf only determinations of leaf area and leaf dry weight, chlorophyll concentration (Ch_{leaf}) and photosynthesis rates (P_N) were measured periodically over the 4-year period. *E. nitens* trees produced the shallowest live crown of the three species, which decreased as planting density increased. Ch_{leaf} declined as planting density increased, but P_N remained the same. *E. nitens* produced the greatest volume and biomass per ha^{-1} of the three species at the end of four years growth. Height increased and stem diameter decreased as planting density increased in *A. cordata*, although stem volume remained about the same. However, planting density did not affect crown volume or Ch_{leaf} in *A. cordata*, but P_N declined as density increased. Trees of *P. sitchensis* grew more slowly than those of the other species during the four-year period, but it produced the densest crown at all planting densities. Competition effects were apparent at leaf level in *P. sitchensis*. Planting density did not affect the above-ground biomass in *A. cordata* or *P. sitchensis,* which was similar for the two species and was lower than that recorded for *E. nitens*. Of the three species examined, *E. nitens* was the most productive at all planting densities.

4.1 Introduction

Short rotation forestry (SRF) systems employ fast growing species to rapidly exploit growing site potential, thus maximising productivity over a short rotation. Selecting a species suited to a site's conditions, as well as applying intensive management practices, are needed to maintain such productivity and yield in any plantation (Ceulemans and Deraedt, 1999).

The three species included in the trial were shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière). *E. nitens and P. sitchensis* were selected for study because they are known to grow well in Ireland (McCarthy, 1979). However, very little literature is available that describes the growth and productivity of *A. cordata*.

Species differ in their responses to varying degrees of competitive stress. This may be reflected in physiological responses leading to changes in resource allocation, resulting in morphological differences. Variations in planting density affect tree physiological activity through competition for resources, e.g. for water, light or nutrients (Toillon et al., 2013). Ultimately competition will be mostly for light, provided soil conditions are favourable and water and nutrient availability are sufficient. Competition will inevitably lead to mortality as weaker plants fail to compete, which is often known as self-thinning. In conventional forestry systems, management aims to control such mortality and utilise the individuals which otherwise would have died. Trees managed in SRF systems are not usually thinned. SRF systems may utilise high density planting to maximise site exploitation at an early stage, but without causing excessive self-thinning after canopy closure.

The standard spacing recommended by DAFM (Forest Service, 2015) for trees planted under the SRF, Forestry for Fibre Scheme, is 2×2 m. Similarly, Neilan and Thompson (2008) recommended a 2×2 m spacing for eucalyptus species grown for biomass under SRF systems. This recommendation was not based on scientific information but was apparently based on extrapolations from data provided from conventional forestry trials over long rotations.

In closely spaced stands, as competition from neighbouring trees increases, tree morphology and physiology often changes in response to avoid shade (Aphalo and

Ballare, 1995). Higher stocking accentuated competition for light in *E. nitens* (Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003) and in *P. sitchensis* (Jack, 1971) and resulted in taller trees. In other studies higher stocking reduced stem diameter increment, but mean height was less affected, such as in stands of eucalyptus (Forrester et al., 2010) and *A. rubra* (Bormann and Gordon, 1984). Thus, the higher planting density used increases the rate at which the crop can utilise a site's resources and generally has important implications for individual tree size. A compromise must be made between maximising individual tree size and stand production (Pinkard and Neilsen, 2003). This can only be achieved by first understanding the specific response characteristics to competition induced by higher planting density, particularly during the early growth period. Competition dynamics during such early stages of tree development have often been overlooked in conventional forestry systems, however this is a period of key importance for SRF.

The aim of this study was to examine the effects of planting density during the early juvenile growth period on the physiological and morphological responses of the three species during the first 4 years after planting. The objectives of the study were to:

- examine how planting density effects growth characteristics of field-grown trees during early juvenile growth (up to 4 years);
- determine the effect of planting density on photosynthesis rates and chlorophyll concentration;
- characterise the effect of competition from planting density on the productivity of each species.

4.2 Materials and methods

4.2.1 Location and site

The study site was located at the Teagasc Environment Research Centre, Johnstown Castle, Co. Wexford (52°17'33.7" N 6°31'42.4" W, 70 m ASL). Mean annual rainfall in the area for 2014 to 2017 was 86.5 mm. Mean air temperature in the same period ranged from -2.1˚C to 23.3˚C (weather data was obtained from the Met Eireann synoptic weather station at Johnstown Castle) (Table 4-1).

The 3-ha site has a gley soil (Table 4-2). The site is prone to waterlogging and the soil has a compacted layer at approximately 50 cm depth. The north side of the site was previously used for grazing cattle; the south side was abandoned agricultural land. Some vegetation control was carried out to maximise the likelihood of establishment, but no fertilisation or irrigation was applied during the trial period. To reduce the likelihood of damage to the trees from farm animals, deer and rabbits, the perimeter of the trial site was fully enclosed with 2 m high galvanized stock fencing with additional rabbit fencing at the base.

Soil pH and nutrient analysis was carried out in 2017. A soil auger was used to obtain soil samples to a depth of 30 cm. The values were benchmarked against Johnston (2005) classification system. Samples were analysed for phosphorus (P), potassium (K), magnesium (Mg), copper (C), manganese (Mn) and zinc (Zn) at Southern Scientific Services, Farrenfore, Co. Kerry (Table 4-3). High levels of magnesium and low to very low levels of phosphorus, potassium and zinc were found. Soil pH was 6.3.

Volumetric soil moisture was measured monthly from June 2016 to Jan 2017. A theta probe and moisture meter (Delta-T Devices Ltd., Cambridge, UK) was used to test soil moisture at 5 locations per plot (see 4.2.3). Soil moisture was systematically sampled so that all plots were represented, but sampling points were always located between trees.

Table 4-1: Climate data at trial site, 2014 - 2017.

Climate		2014 (˚C)	2015 (˚C)	2016 (˚C)	2017 (˚C)
Temperature	mean annual (˚C)	10.6	10.0	10.6	10.4
	annual maximum (˚C)	23.3	22.1	22.9	23.3
	annual minimum (˚C)	-0.7	-1.8	-1.5	-2.1
Precipitation	mean annual (mm)	96.2	88.6	80.9	80.2
	minimum (mm)	196.7	266.9	142.1	160.8
	maximum (mm)	16.3	21.9	44.1	17.5

Table 4-2: Soil characterisation at trial site, Johnstown Castle, Co. Wexford.

Soil	Detail
Soil type	Gley
Soil depth	Hard and compacted soil at 50 cm
Soil pH	6.3
Soil fertility	Table 4-3

Table 4-3 Soil nutrients were assessed at the Johnstown Castle trial site in in 2017. Soil samples were taken from each of the five blocks (80 samples per block) and analysed for phosphorus (P), potassium (K), magnesium (Mg), copper (C), manganese (Mn) and zinc (Z). The soil nutrient levels recommended for forestry by Johnston (2005) are shown at the bottom of the table (minimum requirements).

Block	**P** (mg l^{-1})	**K** (mg l^{-1})	**Mg** (mg l^{-1})	**C** (mg l^{-1})	**Mn** (mg l^{-1})	**Zn** (mg l^{-1})
1	3.8	83.7	210.0	2.2	153.2	1.5
2	1.6	61.9	184.7	1.7	112.8	0.7
3	1.7	53.5	182.7	1.2	54.9	0.6
4	1.0	53.6	137.7	2.0	126.8	0.8
5	0.9	44.3	126.0	1.6	25.6	0.9
Minimum requirements	8	150	100	3	120	3

4.2.2 Site preparations, plant material and planting

The site was ripped and planted from 30th June to 4th July 2014. Both *A. cordata* and *P. sitchensis* were supplied as bare rooted seedlings whereas *E. nitens* were supplied as containerised plug seedlings (Table 4-4Table 4-4). All species were slit planted.

4.2.3 Study design

The experiment was arranged in a randomised block design with four planting density treatments per species (Table 4-5). Two of these treatments were common to all species (0.5×0.5 m and 2×2 m) but the other treatments were unique to each species. The four treatments were replicated once in each of the five blocks. All plots comprised a central measurement area surrounded by a buffer zone, i.e. each plot had a minimum of 12 plants completely surrounded with a buffer of trees of the same species.

Table 4-4: The provenance details, nursery, origin and height at planting of the three species included in the trial.

Binomial name	Common name	Seed origin	Provenance code	Plant description†	Nursery	Height (m) at planting	
Eucalyptus nitens	Shining gum	New Zealand	EI-NZ-M56	1-year old plugs	Irish plant propagators Ltd.	Min Max Mean	0.15 0.44 0.29
Alnus cordata	Italian alder	United Kingdom	AL-UK403-M55	2-year-old seedlings (2+0) bare roots	None-So-Hardy Ltd	Min Max Mean	0.55 1.40 0.94
Picea sitchensis	Sitka spruce (Washington improved)	Denmark	IW-DK-A3365	3-year-old transplant (2+1)	Coillte	Min Max Mean	0.25 0.73 0.45

† Plug plants (P) are seedlings grown in individual cells and transplanted with roots already bound in a plug of medium.
2+0 seedlings were grown for 2 year in a seed bed and were undercut
2+1 seedlings were grown for 2 years in a seed bed and 1 more year in a transplant bed

Table 4-5: A description of sample plots, spacings, stocking densities and the arrangement of the measurement trees within each plot.

Species	Spacing (m)	Stocking density per ha^{-1}	Lines × rows	No. trees measured	Total number of trial trees
A. cordata	2×3	1,333	5×4	20	100
	2×2	2,500	5×5	25	125
	1×1	10,000	4×4	16	80
	0.5×0.5	40,000	4×4	16	80
E. nitens	2.5×3.0	2,500	4×4	16	80
	2×2	1,667	5×5	25	125
	1×1	10,000	4×4	16	80
	0.5×0.5	40,000	4×4	16	80
P. sitchensis	2×2	2,500	4×3	12	60
	1×2	5,000	5×3	15	75
	1×0.5	20,000	4×4	16	80
	0.5×0.5	40,000	4×4	16	80

4.2.4 Establishment

Mortality rates were high in the first 7 months after planting in *E. nitens* (24% mortality) and *A. cordata* (68%), but few of the *P. sitchensis* seedlings died (4%) (Table 4-6). There was shoot dieback and hare damage to *A. cordata* trees, but the exact cause of the dieback could not be determined. The mean precipitation was 35.2 mm, mean air temperature 14˚C with a minimum of 6.8˚C and a maximum of 22.9˚C during the week of planting.

The dead plants were removed and replaced with other plants from 29th April 2015 to 7th May 2015, using additional plants from the same consignment that had been heeled-in on site or from the plot buffer zone. The buffer zone trees were replaced with new plants of the same species and provenance, but these seedlings were not part of the original consignment. Plants were not replaced after 9th July 2015 and natural mortality was recorded. High winds in the winter of 2015/2016 and 2017 caused some damage, but mostly to *E. nitens,* with about 15% (30/365) of the tree affected.

Table 4-6 Mortality rates after 7 months and in January 2018, including number of dead plants and percentage of mortality.

Species	No. dead plants after 7 months	Mortality %	No. dead plants after 4 years	Mortality %	Original stocking and (trial end)
E. nitens	88	24.1	30	15	385(355)
A. cordata	263	68.3	7	2	365(358)
P. sitchensis	13	4.4	5	2	295(290)
Total mortality	364	34.7	42	4	1049(1007)

4.2.5 Measurements and observations

4.2.5.1 Leaf and branch selection

Sun and shade leaves may exhibit differences in growth and physiological responses (Salisbury, 1928). Results from the polytunnel experiment revealed photosynthesis, chlorophyll concentration, leaf area and leaf dry weight measurements of shade leaves were more sensitive to changes in planting density than sun leaves (Chapter 3.3). Therefore, only shade leaves were selected for study.

The response to light intensity (i.e. photosynthetic light response curves) was examined to determine the best crown position for sampling shade leaves (Chapter 3.4.1.2). An index was used to identify leaves of similar maturity, based on the position from the stem or branch tip using the leaf plastochron index (LPI) (Chapter 3.3.3.1).

Table 4-7: Measurements of photosynthetic activity, chlorophyll concentration and specific area were carried out through the growing season on leaves of similar developmental stage. A consistent location for measurement was indicated using a plastochron index. Branches (B) were counted from the top of a tree. Leaves (L) were counted from the branch/stem growing tip. In *P. sitchensis* whorl branches were selected.

	Photosynthesis	**Chlorophyll concentration**	**Specific leaf area (3 × leaves)**
E. nitens	B06-L05	B08-L05	B02-L03, B04-L05, B07-L07
A. cordata	B06-L06	B08-L06	B03-L03, B05-L05, B08-L07
P. sitchensis	-	-	1st, 3rd, Bottom whorl (one-year-old growth)

4.2.6 Physiological measurements

4.2.6.1 Chlorophyll concentration

Leaf chlorophyll concentration (mg m^{-2}) (Ch_{leaf}) was determined using a chlorophyll concentration meter (Opti-Sciences® CCM-300; Opti-Sciences Inc., NH, USA). Ch_{leaf} was measured in July, August and September 2017 in *A. cordata* and *E. nitens*. Readings were obtained from three leaves (Table 4-7) on three randomly chosen trees per plot. Five measurements were taken on the adaxial surface of leaves near the centre of the lamina, avoiding the margins and midrib. The mean of these readings was used in the analysis. Chlorophyll concentration was not measured in *P. sitchensis* because the results of the previous experiment (Chapter 3.4.1.1) showed that planting density had no effect on Ch_{leaf} in that species.

4.2.6.2 Photosynthetic activity

Leaf level gas exchange measurements were performed using a portable photosynthesis system (Li-Cor LI-6400XT; Li-Cor Biosciences; Lincoln, USA) with an LED light source (Li-Cor LI-6400-02) in *A. cordata* and *E. nitens*. Photosynthesis measurements were carried out during August and September 2017 on fully expanded mature, undamaged shade leaves (section 3.3.3.1) on three *E. nitens* and *A. cordata*

trees per plot. Leaves were selected using the LPI (Table 4-7) protocol described in section 4.2.5.1 above.

The chamber temperature in the LI-6400XT was set to the mean for the previous month in the area and was obtained from Met Eireann Johnstown Castle meteorological station. The following measurement protocol was used for the LI-6400XT: PAR level of 1,000 µmol (photon) m^{-2} s^{-1} with a chamber temperature of 15°C; leaf fan was at maximum (5); air flow rate used was 500 mml with a CO_2 concentration of 400 ppm. The LI-6400XT uses two infra-red gas analysers (IRGA's) in the LI-6400 referred to as (sample and reference). CO_2 was controlled on reference IRGA.

Measurements of photosynthesis were not carried out on *P. sitchensis,* mainly because of time constraints (e.g. needle leaves are more difficult to assess).

4.2.7 Morphological measurements

Stem height (m) and root collar diameter, RCD (cm) (measured 5 cm above soil level) were determined immediately after planting in 2014 and in January each year from 2015 to 2018. Stem volume, (SV) was determined using RCD and height.

$$SV = (\pi \times RCD \times (H/3)) \quad \text{(Eq. 5)}$$

where SV = stem volume (m^3), RCD = root collar diameter (cm). Crown height CH (m) was determined from soil level to lowest living branch. A living branch was defined as a branch containing green (chlorophyll) colour, as observed upon lightly scraping the bark. The base of the live crown was defined as the place of insertion of the lowest live branch (Soares and Tomé, 2001). The length of the longest branch on the tree in each cardinal direction was measured in September 2017. Mean branch length (BL) and stem height were used to determine the height to branch length ratio. Crown depth and mean branch length were used to determine the crown volume CV (m^3) (Eq. 6).

$$CV = (\pi BL^2 (CD/3)) \quad \text{(Eq. 6)}$$

where *CV* = crown volume (m^3), BL^2 = mean branch length. Branch basal diameter (cm) was determined on the longest branch prior to the destructive harvest in 2018. The projected crown area or the estimated spread of the crown for each tree was calculated (Eq. 7) using the mean BL:

$$PCA = \pi BL^2 \quad \text{(Eq. 7)}$$

where *PCA* = projected crown area (m^2). DBH (cm) was measured in 2018 when the height of most of trees was above 1.3 m.

4.2.7.1 Specific leaf area

Leaf area measurements were carried out during July 2018. Nine leaves (*E. nitens* and *A. cordata*) or thirty needles (*P. sitchensis*) were removed from one tree per plot for each species. Leaves were sampled from top, middle and bottom branches. The LPI was used to identify comparable leaves (as the same developmental stage) in each crown section (3.3.3.1 above). The leaves and needles were scanned on a flatbed scanner (DCP-770CW; Brother Industries Ltd, Manchester, UK). Leaf surface area was calculated using leaf area measurement software (Easy Leaf Area) (Easlon and Bloom, 2014). The leaves were dried at 70˚C until a constant dry weight was obtained. Specific leaf area (SLA) (Eq. 8) was calculated:

$$SLA\ (cm^2 g^{-1}) = LA\ (cm^2)/DW\ (g) \quad \text{(Eq. 8)}$$

where *SLA* = specific leaf area ($cm^2\ g^{-1}$), *LA* = leaf area (cm^2) and *DW* = dry weight (g).

4.2.7.2 Leaf area index

Leaf area index (*LAI*) was defined by Watson (1947) as the total one-sided area of leaf tissue per unit ground surface area. The leaf area index of each tree was determined through the product of total leaf *DW* and *SLA* (Eq. 8) (White et al., 1994).

$$LAI = SLA/total\ Leaf\ DW \quad \text{(Eq. 9)}$$

4.2.8 Leaf nutrient analysis

Samples of leaves and needles (2 g per tree) were obtained through random selection of the leaves used to estimate biomass. The samples were sent to Southern Scientific Laboratory. Co. Kerry, for analysis of N, P and K.

4.2.9 Biomass measurements

Tree form and mortality were assessed in December of 2017 (Table 4-8). A proportion of trees had died or had been damaged, presumably as a result of the severe storms. After 4 years growth, 12% of the trees were damaged or dead, while 16% were forked in the upper crown, leaving 72% with upright straight form. This resulted in many gaps in the canopy providing more space for the remaining trees, potentially compromising the experiment. A sampling protocol was adopted to minimise the potential effects of bias due to these effects (Table 4-8). The selected trees had to be surrounded with living trees which had a height and diameter within ± 1 SD of the plot mean. Trees suitable for sampling had to have a single upright stem. Only the originally planted trees were considered; the trees replaced in 2015 were excluded. Trees which were wind-blown in the winter of 2015/2016 storm, which were bent and still alive, were not included. The trees for harvesting were chosen close to the centre of each plot.

Table 4-8: Selection criteria for harvest sampling where each tree complies with a minimum criterion (†); neighbouring trees present >= 6, original = 1, windthrow = 2 or 0, tree form = 1, stem form = 1.

Neighbours present	Designation	Original or replaced	Designation	Windthrow	Designation
None	0	Original	1†	2016 storm	1
One	1	Replaced	2	Ophelia	2
Two	2			Not affected	0†
Three	3				
Four	4				
Five	5				
Six	6†				
Seven	7				
Eight	8				

Tree form	Designation	Stem form	Designation
Dead	0	Dead	0
Full single stem	1†	Upright	1†
Half stem	2	Bent	2
No stem, branched from base	3	Horizontal but alive	3
Poor/Dying overall	4	Over 45˚	4

Three trees per plot were harvested in January 2018. Three discs, each 10 cm wide, were cut from each stem to determine wood density (as described below). Discs were cut from the stems at 20%, 40% and 60% of tree height. The numbers of 1st order branches were recorded for each tree in advance of the harvesting operations. Trees were cut at ground level and tree biomass was divided into stem, branch and foliage components. Above-ground biomass (AGB) included stem, branches and leaves. Branch biomass included the reproductive tissues (e.g. catkins) in *A. cordata.* All branch and leaf components were dried at 70ºC until a constant DW was determined (Proe et al., 2002).

The separation of needles from branches in *P. sitchensis* was considered too time consuming. Therefore, sub-sections of branch and needle components were selected and were used to calculate the ratio of these components to total biomass. Branches were placed into three groups according to the position on the stem (top, middle and bottom) and weighted. A small sub-section of biomass was taken from the top, middle and bottom groups. Using the sub-section, needles were separated from branch wood and weighted. All components were oven dried at 70˚C until a steady dry weight was achieved.

The foliage of *E. nitens* was separated from the branches before drying. However, *E. nitens* leaves harvested in January had to be excluded as salt damage from recent winter storms had damaged a portion of leaves in the upper crown. *A. cordata* had no leaves at the time of the January sampling. Leaf biomass was collected during a second harvesting of *E. nitens* and *A. cordata* trees in July (one tree per plot), which was used to calculate leaf biomass (Eq. 10) using a regression equation. As only one tree was selected per plot, regression equations were used to apply the leaf biomass to the all trees of each species in the trial using diameter as a predictor.

$$AGB_i = \beta_1 RCD^{\beta_2} \qquad \text{(Eq. 10)}$$

where *AGB* = above ground biomass (kg); *i* = tree component (stem, branch leaf); *RCD* = root collar diameter (cm); and β_1, β_2 = fitted coefficients (Annighöfer et al., 2016).

4.2.9.1 Wood density

Specific gravity (SG) of wood is defined as the density of wood relative to the density of water (Williamson and Wiemann, 2010). The specific gravity or wood density of the three-disc samples per tree was assessed (Eq. 13) (including bark and pith). Green volume was measured using the water displacement procedure described by Olesen (1971). Discs were oven-dried at 105˚C until a steady dry weight was obtained (Williamson and Wiemann, 2010).

4.2.9.2 Plot level biomass estimation

To estimate stand-level biomass, allometric equations were developed using independent variables to predict total biomass (Eq. 11, 12). Biomass was estimated using the power law developed by Snell (1892), which provided the best fit to the data. Analysis was performed in SAS® statistical analysis software (SAS statistical analysis software 9.4; SAS Institute, Cary, NC, USA, 1988) with the NLMIXED procedure. Foliage DW per plot was obtained through non-linear power law:

$$Ln(AGB^{x})^{\,tree} = \beta_1\, LnRCD^{\,\beta 2} \qquad \text{(Eq. 11)}$$

where AGB^x = above-ground component (stem, branch, foliage) (g); *RCD* = root collar diameter (cm); and *β1* and *β2* = fitted coefficients. The results were back-transformed and stand level biomass calculated using the following equation:

$$(AGB^{x})^{stand} = (meanAGB^{x})^{\,tree} \times\ no.stems\ per\ plot \qquad \text{(Eq. 12)}$$

where no. stems per plot = the number of stems alive at the end of the trial.

$$SG = ODM/green\ volume \qquad \text{(Eq. 13)}$$

where *SG* = specific gravity; *ODM* = oven dry mass (g).

4.2.10 Data analysis

The data were checked for normality and homogeneity of variance and data log transformations were applied to measurements of stem height, root collar diameter, branch length, crown volume, crown depth and biomass in *E. nitens.* The effect of planting density on morphological measurements were analysed using an ANOVA with the Proc Glimmix. The effect on biomass was analysed, with Proc NLMixed (procedure for nonlinear mixed models) for non-linear regression, using diameter to predict plot values. Planting density effects on SLA and LAI per plot were analysed using ProcMixed (procedure for mixed models), with root collar diameter as plot predictor. A significance level of $p < 0.05$ was applied. The biomass allocation percentage data were normally distributed so were not transformed.

4.3 Results

4.3.1 Soil moisture

Plot soil moisture levels were measured monthly from June 2016 to January 2017. Soil moisture was lowest in mid-August, increasing gradually to the highest values in mid-December. At the highest planting density (0.5×0.5 m), soil moisture was significantly lower (Table 4-9) than at the lower planting densities of 1×1 m and 2×2 m in the *A. cordata* plots (Figure 4-1). Species and planting density had no impact on soil moisture levels in the *E. nitens* or *P. sitchensis* plots.

4.3.2 Physiological responses

Chlorophyll concentrations were not assessed in *P. sitchensis* in the field as results from the polytunnel experiment (Chapter 3.3.1) showed that planting density effects were not significant. Photosynthesis was not measured in *P. sitchensis* due to the small size of the branches.

Table 4-9: Repeated measures ANOVA with soil moisture volume percentage recorded over nine months from June to January in *E. nitens*, *A. cordata* and *P. sitchensis* with four planting densities. Values in bold indicate significance at p ≤0.05.

Soil moisture		*E. nitens*		*A. cordata*		*P. sitchensis*	
	df	F	P	F	p	F	P
Block	4	5.7	**0.0083**	2.5	0.0982	5.8	**0.0076**
Planting density	3	2.2	0.1401	11.7	**0.0007**	0.6	0.6568
Month	8	90.3	**<.0001**	112.1	**<.0001**	115.9	**<.0001**
Month x planting density	24	0.8	0.7385	1.6	0.0613	1.3	0.1802

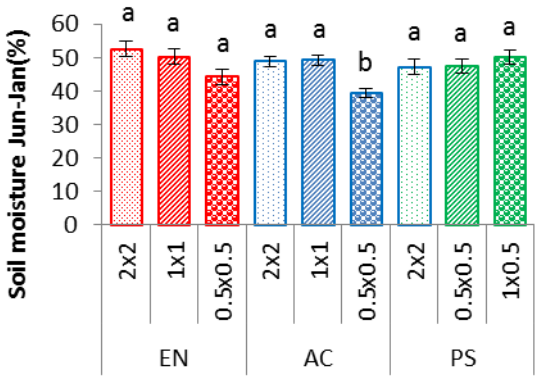

Figure 4-1: Variation in soil moisture (% volume) during the period June 2016 to January 2017 in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) planted at four spacings. Vertical lines = ±SE of the mean. Different letters indicate significant differences (p ≤0.05) with planting densities within species.

4.3.3 Chlorophyll concentration

The Ch_{leaf} varied significantly ($p < 0.0001$) between species with *A. cordata* containing a higher concentration than *E. nitens*. Ch_{leaf} increased significantly from July to August in *A. cordata* but did not change with planting density. *E. nitens* leaves contained significantly lower Ch_{leaf} at the higher planting density (Table 4-10). The date of measurement (July, August and September) did not affect Ch_{leaf} in *E. nitens* (Figure 4-2).

Table 4-10: Repeated measures ANOVA of the effects of planting density and measurement date on chlorophyll concentration (mg m²) in *E. nitens* and *A. cordata* in field trials during July, August and September. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*	
Chlorophyll concentration	df	F	P	F	p
Block	4	12.0	**0.0051**	2.0	0.1912
Planting density	2	9.5	**0.0140**	0.2	0.7967
Month	2	5.1	0.0505	9.1	**0.0087**
Month x planting density	4	0.9	0.4987	0.6	0.6807

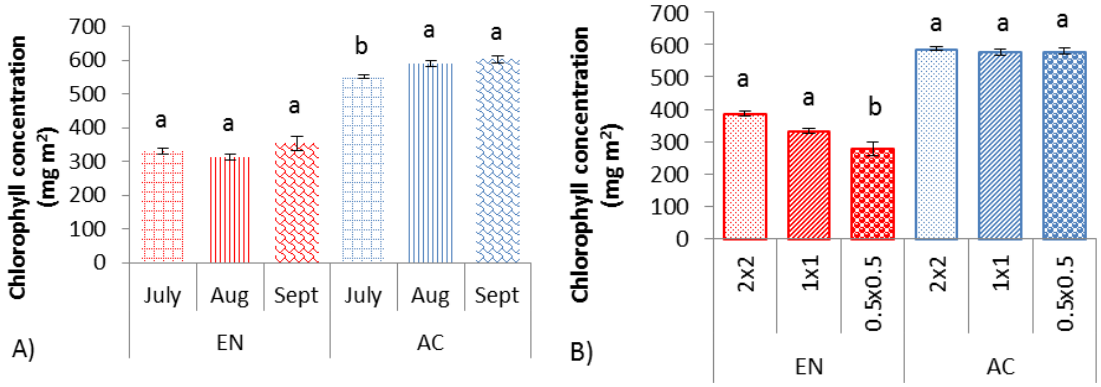

Figure 4-2: Mean leaf chlorophyll concentration in July, August and September 2017 with (A) variation in planting density per month and (B) accumulated data over the three months per planting density in *E. nitens* (EN) and *A. cordata* (AC). Vertical lines = ±1 SE of the mean. Different letters indicate significant differences (p <0.05), (A) with months within species and (B) in response to planting density within species.

4.3.4 Photosynthetic rates

Photosynthesis rates (measured at PAR 1000 µmol m^{-2} s^{-1} in shade leaves only) varied significantly with planting density in *A. cordata* but not in *E. nitens* (Table 4-11). The rate of photosynthesis was significantly lower at the highest planting density in *A. cordata* (Figure 4-3). Transpiration rates also declined significantly as planting density increased in *A. cordata.* There was no effect of planting density on transpiration rates in *E. nitens*. Planting density had no effect on stomatal conductance or intercellular CO_2 concentration (data not shown) in *A. cordata* or *E. nitens*.

Table 4-11: Repeated measures ANOVA of the effects of planting density and month on photosynthesis and transpiration rates in *E. nitens* and *A. cordata* at a light intensity of PAR 1000 µmol m^{-2} s^{-1}. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*	
	df	F	P	F	p
Photosynthesis rates					
Block	4	4.24	0.0573	0.55	0.7067
Planting density	2	3.65	0.0916	9.38	**0.0080**
Month	1	1.02	0.3511	0.20	0.6667
Month x planting density	4	0.24	0.7922	0.27	0.7719
Transpiration rates					
Block	4	2.59	0.1430	3.02	0.0861
Planting density	2	0.56	0.5978	7.29	**0.0157**
Month	1	3.20	0.1241	8.22	**0.0209**
Month x planting density	4	0.13	0.8800	0.07	0.9371

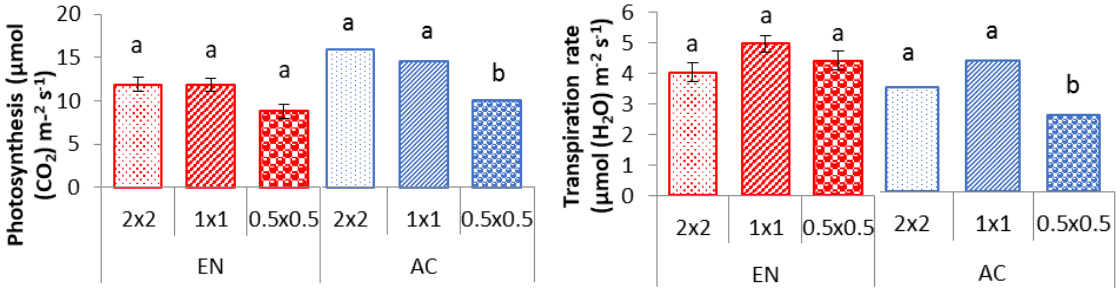

Figure 4-3: Photosynthesis and transpiration rates at PAR 1,000 µmol m^{-2} s^{-1} in response to planting density in *E. nitens* (EN) and *A. cordata* (AC). Vertical lines = ± SE of the mean. Different letters indicate significant differences (p ≤0.05) with densities within species.

4.3.5 Morphological measurements

Tree height increased and root collar diameter decreased significantly as planting density increased in *A. cordata* (Figure 4-4). Branch diameter decreased significantly as planting density increased in *A. cordata*, while branch length was not affected. Planting density had no effect on height, root collar diameter, branch length or branch diameter in *E. nitens* and *P. sitchensis* (Table 4-12). Planting density did not affect diameter at breast height, crown depth or the number of live branches in all species (Table 4-13). The number of branches to height ratio was highest in *P. sitchensis*.

Table 4-12: Mean values for a range of morphological parameters in *E. nitens*, *A. cordata* and *P. sitchensis*. Different superscript letters indicate significant differences with treatments p ≤0.05.

Variable	*E. nitens*			*A. cordata*			*P. sitchensis*		
	2×2	1×1	0.5×0.5	2×2	1×1	0.5×0.5	2×2	1×0.5	0.5×0.5
Stem height (m)	3.6^{a}	3.1^{a}	3.3^{a}	2.3^{ab}	2.5^{ab}	2.7^{a}	1.6^{a}	1.9^{a}	1.9^{a}
RCD (cm)	5.6^{a}	3.9^{a}	3.1^{a}	4.5^{a}	4.3^{ab}	3.7^{b}	3.3^{a}	3.3^{a}	3.0^{a}
DBH (cm)	3.8^{a}	2.5^{a}	2.0^{a}	1.8^{a}	1.8^{a}	1.8^{a}	1.4^{a}	1.8^{a}	1.5^{a}
Branch length (cm)	90.1^{a}	66.0^{a}	52.7^{a}	111.2^{a}	111.9^{a}	100.6^{a}	50.1^{a}	56.0^{a}	55.2^{a}
Branch diameter(cm)	1.4^{a}	0.8^{a}	0.7^{a}	1.8^{a}	1.3^{ab}	1.1^{b}	1.0^{a}	0.9^{a}	0.7^{a}
Branch count (live)	23.8^{a}	19.4^{a}	20.5^{a}	32.1^{a}	31.6^{a}	23.3^{a}	70.9^{a}	73.2^{a}	69.7^{a}
Branch count (dead)	12	11	11	0	0	0	0	0	3
Crown height (m)	0.9^{a}	1.3^{a}	1.8^{a}	0.4^{a}	0.4^{a}	0.6^{a}	0.3^{a}	0.3^{a}	0.3^{a}
Crown depth (m)	2.7^{a}	1.9^{a}	1.7^{a}	1.9^{a}	2.1^{a}	2.2^{a}	1.4^{a}	1.5^{a}	1.5^{a}
Stem volume (m^3)	0.2^{a}	0.2^{ab}	0.1^{b}	0.1^{a}	0.1^{a}	0.1^{a}	0.1^{a}	0.1^{a}	0.1^{a}
Height: branch ratio	40.4^{b}	48.5^{b}	59.6^{a}	23.3^{b}	24.2^{b}	29.7^{a}	31.2^{a}	30.5^{a}	34.3^{a}
Crown volume (m^3)	4.3^{a}	1.3^{a}	0.7^{a}	2.9^{a}	2.9^{a}	2.4^{a}	0.4^{a}	0.7^{a}	0.6^{a}
Crown depth % of height	62.7^{ab}	56.7^{ab}	48.3^{b}	83.4^{a}	83.4^{a}	80.5^{a}	81.3^{a}	81.6^{a}	81.9^{a}
Projected crown area (m^2)	3.1	1.5	0.9	4.1	4.0	3.2	0.8	1.1	1.0

Table 4-13: ANOVA of the effects of planting density on tree height, root collar diameter, diameter at breast height, branch length, branch diameter, stem volume, height: branch ratio, crown volume, crown depth (% of total height) and crown area, and projected crown area in *E. nitens, A. cordata* and *P. sitchensis*. *E. nitens* height, root collar diameter, branch diameter, crown depth % of height data were log transformed. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
Planting density	***df***	***F***	***p***	***F***	***P***	***F***	***p***
Height	3	0.6	0.6629	4.1	**0.0320**	1.0	0.4141
RCD	3	1.8	0.2151	4.3	**0.0288**	0.2	0.9040
DBH	3	2.2	0.1615	0.1	0.9640	0.9	0.4682
Branch length	3	4.1	0.0604	1.2	0.3398	0.4	0.7747
Branch diameter	2	2.9	0.1316	7.1	**0.0172**	4.2	0.0566
Branch count	2	0.7	0.5440	3.8	0.0693	0.1	0.9229
Crown height	3	2.1	0.1998	3.3	0.0882	1.8	0.2239
Crown depth	3	2.3	0.1495	2.3	0.1292	0.9	0.4682
Stem volume	3	7.7	**<.0001**	0.5	0.6568	2.5	0.0636
Height: branch ratio	3	21.6	**<.0001**	10.0	**<.0001**	2.6	0.0600
Crown volume	3	2.8	0.1012	0.9	0.4858	1.1	0.4014
Crown depth % of height	3	3.9	**0.0497**	2.1	0.1497	0.0	0.9953
Projected crown area	3	2.1	0.0999	1.3	0.3320	0.5	0.6684

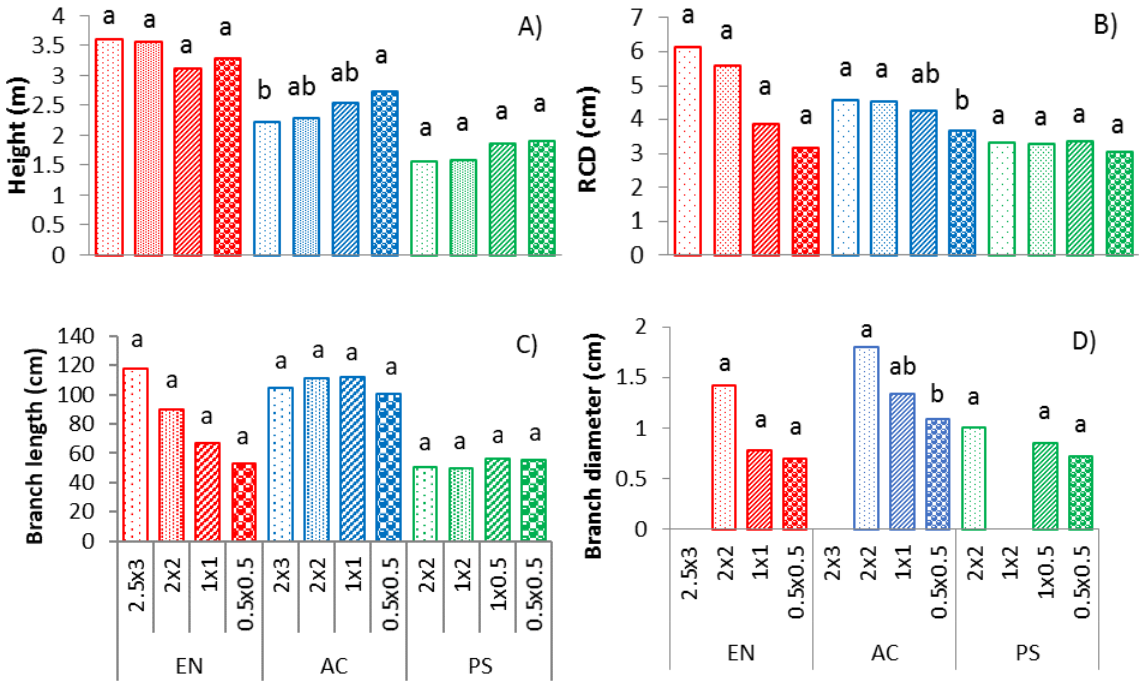

Figure 4-4: Mean of A) height (m), B) root collar diameter (cm) C) branch length (cm) and D) branch diameter (cm) response to planting density in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). The lowest planting density is omitted from branch diameter; 2×2 m spacing was included in *P. sitchensis* to allow for inter-species comparisons. SE not presented as data in *E. nitens* was transformed. Different letters indicate significant differences (p <0.05) in response to planting density within species.

The height: branch length ratio significantly increased as planting density increased in *E. nitens* (Figure 4-5). The height: branch ratio was similar at the 2×3, 2×2 and 1×1 m density in *A. cordata* but significantly larger at the 0.5×0.5 m density. Planting density had no effect on the height: branch ratio in *P. sitchensis.*

Stem volume remained similar between the two lowest planting densities in *E. nitens* with a mean 0.245 m^3 per tree, and then decreased significantly to 0.100 m^3 at 0.5×0.5 m spacing. Planting density did not affect stem volume in *A. cordata* and *P. sitchensis,* with a mean of 0.110 and 0.06 m^3, respectively.

Crown depth as a percentage of height declined significantly as planting density increased in *E. nitens*, ranging from 71% at 2.5×3 m to 48% at 0.5×0.5 m density. However, crown depth (% of height) was similar across planting densities in *A. cordata* and *P. sitchensis*, ranging from 80 to 83%.

Planting density did not affect crown volume in all species (Figure 4-5), although there were large differences in crown volume between species, with a significantly larger volume ($p < 0.0001$) in *A. cordata* (mean 2.6 m^3) than *P. sitchensis* (mean 0.5 m^3). Although planting density did not affect crown volume in *E. nitens* values varied greatly from 0.7 m^3 at 0.5×0.5 m planting density to 8.5 m^3 at 2.5x3 m^3.

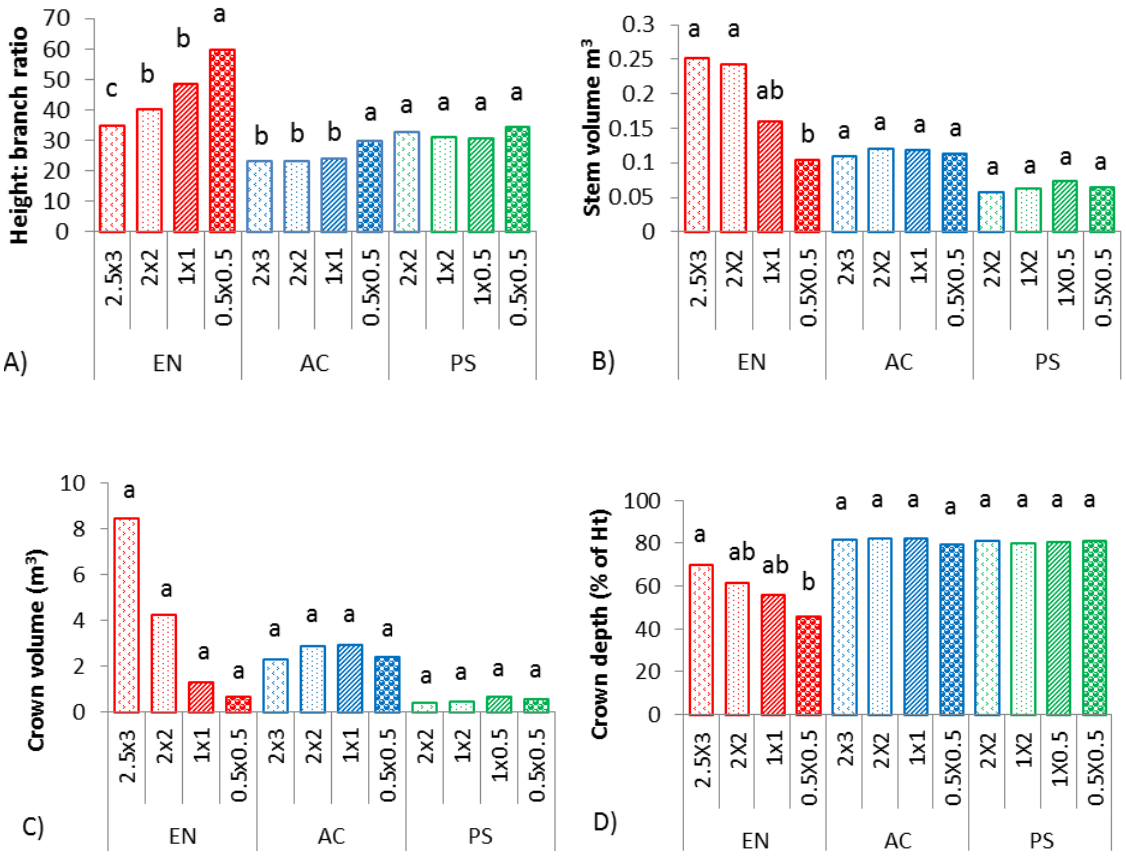

Figure 4-5: A) mean height: branch ratio, B) stem volume m^3, C) crown volume m^3 and D) crown depth (% of total height) in response to planting density in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). SE not presented as data in *E. nitens* was transformed. Different letters indicate significant differences ($p < 0.05$) in response to planting density within species.

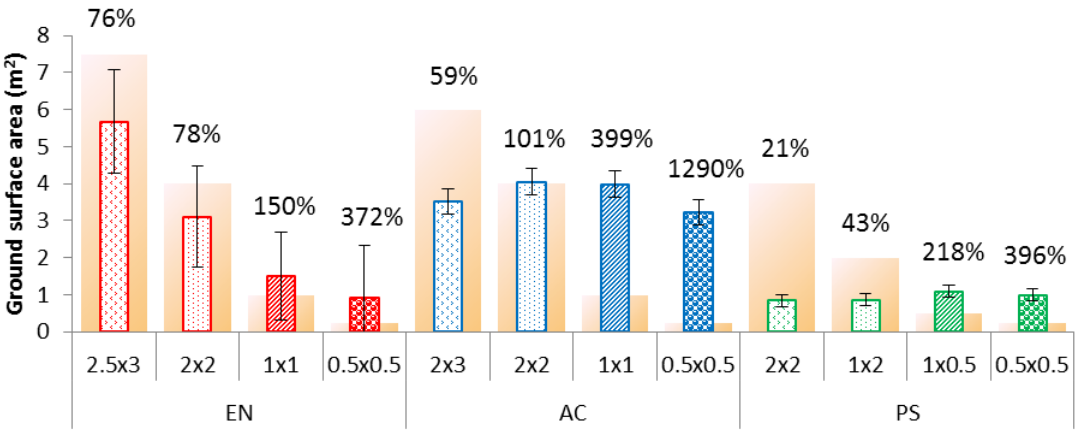

Figure 4-6: Ground planting area (orange bars, m²) overlaid with projected crown area (hatched bars, m²) in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). The differences in growth application in response to planting density within species displayed as percentage projected crown cover per unit area. Vertical lines = ±1 SE of the mean.

Branches grew into the surrounding tree crowns at the 0.5×0.5 m and 1×1 m planting density in *E. nitens* and *A. cordata* and at the 0.5×0.5 m and 1×0.5 m spacing in *P. sitchensis* by the fourth year after planting, as reflected in projected crown area measurements (Figure 4-6). Branches had grown into the neighbouring crowns by as much as 1290% at the highest planting density of 0.5×0.5 m in *A. cordata*. The crowns of *A. cordata* had fully extended over the entire area (i.e. occupied the planting area) at the 2×2 m spacing by the fourth year. In contrast, the crown area did not fully occupy the plot area at the 2×2 m spacing within the same time period in *E. nitens* and *P. sitchensis*. However, at the widest spacing (2×3 m), the projected crown area had occupied 76% of the planting area by the fourth year in *E. nitens*. In contrast, trees planted at the widest spacing (2×3 m) had occupied 59% of the planting area in *A. cordata* and 21% of the planting area at 2×2 m in *P. sitchensis*.

Specific leaf area (SLA) was significantly lower at the lowest planting density in *P. sitchensis* (Table 4-14). Planting density did not affect SLA in *A. cordata* and *E. nitens* (Figure 4-7). SLA was significantly larger in *A. cordata* than in *E. nitens* or *P. sitchensis* across all planting densities. Leaf area index (LAI) increased significantly as planting density increased in *A. cordata*. The LAI was declined significantly from the high to the

medium planting density in *P. sitchensis* but was similar between the medium and low planting density. Planting density did not affect LAI in *E. nitens*. Planting density did not affect the leaf area or leaf dry weight (data not shown) in all three species.

Table 4-14: ANOVA with regression using root collar diameter as plot predictor for SLA and LAI per plot in response to planting density in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
Planting density	df	F	p	F	p	F	p
SLA	2	1.5	0.3041	2.7	0.1289	6.3	**0.0269**
LAI	2	0.8	0.4813	210.7	**<.0001**	12.7	**0.0047**

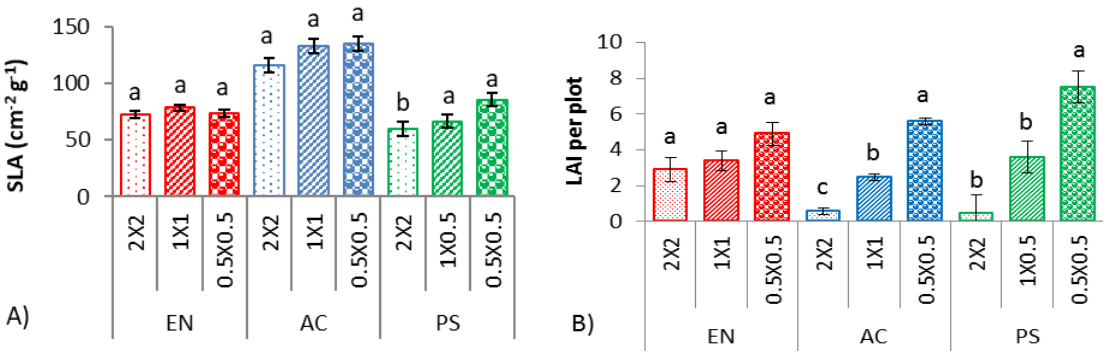

Figure 4-7: SLA and LAI per plot at three planting densities in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). Vertical lines = ±1 SE with negative lower SE set to zero for SS. Different letters indicate significant differences (p <0.05) in response to planting density within species.

4.3.6 Foliage nutrient concentrations

Potassium (K) concentration increased significantly in the leaves of *A. cordata* as planting density increased (Figure 4-8). Nitrogen (N) and phosphorous (P) concentrations were significantly greater in leaves of A. cordata (p <.0001) than in those of *E. nitens* or *P. sitchensis,* which contained similar nutrient levels. Planting density had no effect on N, P or K concentrations in the foliage of *E. nitens* or *P. sitchensis* or on P or N concentrations in *A. cordata*.

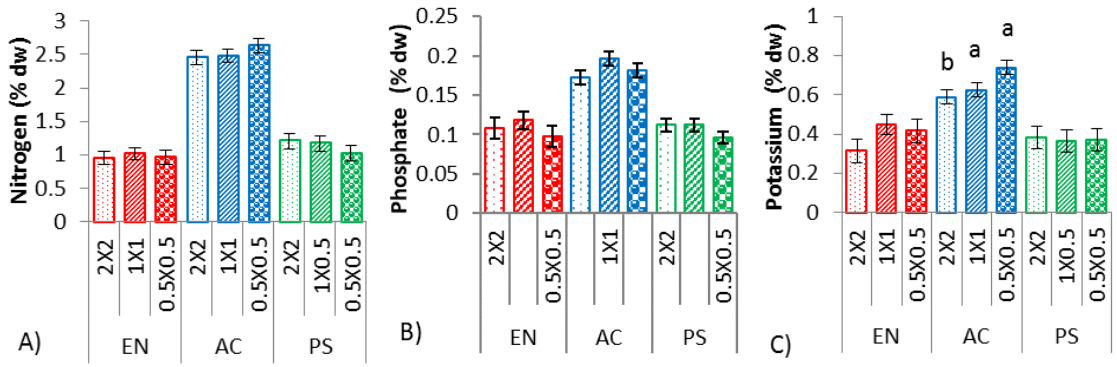

Figure 4-8: Mean A) nitrogen, B) phosphorus and C) potassium concentration (% DW) in the foliage in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) at three plant spacings. Vertical lines = ± SE of the mean. Different letters indicate significant differences (p <0.05) in response to planting densities, within species.

4.3.7 Biomass

The differences in the growth characteristics of the three species at the two highest planting densities were non-significant and therefore tree biomass samples were not selected from trees grown in the higher density treatment.

Branch dry weight decreased significantly as planting density increased in *A. cordata* (Figure 4-9). However, total above-ground biomass, stem and leaf biomass per tree were similar across planting densities (Table 4-15). All biomass values were highly variable in *E. nitens,* particularly at the 2×2 m spacing and no planting density effects were identified (Figure 4-10). *E. nitens* tend to retain dead branches. However, the amount of biomass in the retained dead branches did not significantly change with planting density (data not shown). Planting density did not affect the total above-ground biomass (stem, branch and needle) in *P. sitchensis*.

Table 4-15 ANOVA of above ground, stem, branch, needle/leaf biomass components per tree affected by planting density using allometric regression equation (Eq.8) in *E. nitens*, *A. cordata* and *P. sitchensis*. Above-ground biomass includes bark and bole, branches, leaves and needles. The *E. nitens* data were log transformed. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
Planting density	df	F	p	F	p	F	p
Above-ground	2	1.9	0.2361	3.0	0.1096	0.6	0.5546
Stem	2	2.0	0.2220	1.4	0.3006	0.4	0.7051
Branch	2	2.3	0.1798	5.7	**0.0286**	1.4	0.2994
Needles/leaves	2	2.0	0.2179	0.8	0.4827	0.4	0.6885
Biomass per ha^{-1}	2	4.0	0.0776	150.3	**<.0001**	9.5	**0.0100**

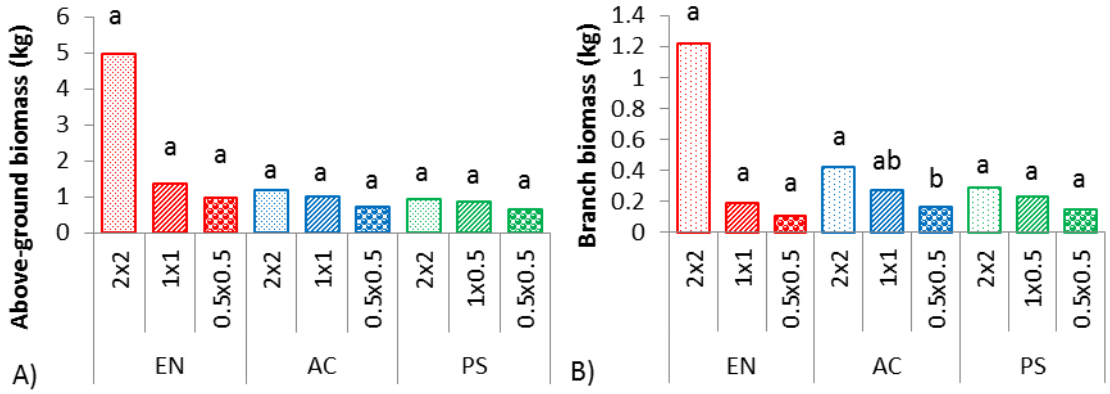

Figure 4-9: Above-ground and branch biomass at three planting densities in *E. nitens* (EN) n=32, *A. cordata* (AC) n=38 and *P. sitchensis* (PS) n=38. *E. nitens* was log transformed. SE not presented as data in *E. nitens* were log transformed. Different letters indicate significant differences (p <0.05) in response to planting density within species.

Regression equations (Eq. 12) for estimating biomass components were used to generate plot level biomass estimations for each species (Table 4-16). DBH is commonly used to predict biomass using allometric models based on data derived from large trees, but root collar diameter fitted the data better in this study. Using these models, the total above-ground biomass was significantly larger at the 0.5×0.5 m spacing in the three species and decreased as spacing increased in *A. cordata* and *P. sitchensis*. Planting density did not significantly affect above-ground biomass in *E. nitens* (Figure 4-10) although total biomass (t ha^{-1}) in *E. nitens* was larger at 2×2 and 0.5×0.5 m spacing than at the same spacings in *A. cordata or P. sitchensis*.

Table 4-16: Allometric equations (Eq. 11 and 12) relating an explanatory variable RCD (cm) to total above-ground biomass (stem, branch and foliage) in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS).

Species	Treatment	Coefficient(β_1)	Power (β_2)	Live stocking ha^{-1}	Stand biomass (t ha^{-1})
			Above-ground biomass		
E. nitens	2x2	0.080	3.809	2400	19.35
	1x1	0.104	3.663	9375	17.84
	0.5x0.5	0.128	3.653	39375	51.56
A. cordata	2x2	0.141	3.161	2500	3.89
	1x1	0.048	5.217	9875	15.72
	0.5x0.5	0.248	1.626	40000	30.20
P. sitchensis	2x2	0.130	3.818	1300	2.70
	0.5x1	0.139	3.714	19750	20.89
	0.5x0.5	0.220	2.655	40000	30.00

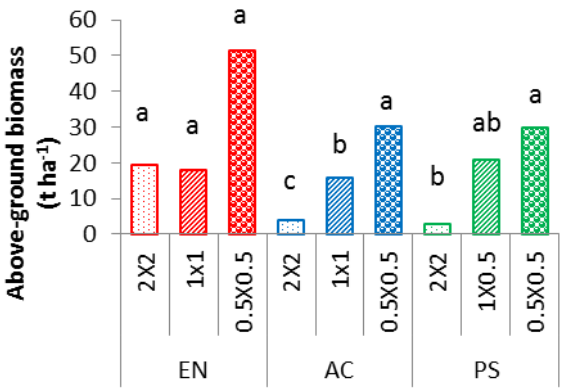

Figure 4-10: Mean above-ground biomass estimations using allometric equations (Eq. 12) in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). SE not presented as data in *E. nitens* were log transformed. Different letters indicate significant differences (p ≤0.05) in response to planting densities within species.

The percentage of biomass allocated to stem, branch and leaf components differed between species (Table 4-17). More biomass was allocated to stem components in *E. nitens* than in the other species. The proportion of biomass allocated to the stem was significantly greater (73%) at the high planting density than at medium (62%) or low density (56%) in *E. nitens* (Figure 4-11). At low spacing, *E. nitens* allocated similar resources to branch and leaf biomass components. The amount allocated to the leaves significantly increased from 19 to 31% at the low to the middle spacing, but leaf biomass significantly declined to 16% at the highest planting density, while branch biomass remained similar across densities.

The proportion of biomass allocated to the stem increased as density increased from 52% at low planting density to 63% at high density in *A. cordata*. Concurrently the amount of biomass allocated to branches, declined from 34% to 23%, but the proportion of leaf biomass did not change with planting density.

Stem biomass was significantly greater than branch or leaf biomass in *P. sitchensis*. The proportion allocated to stem, leaf and branch components did not differ with planting density in *P. sitchensis* with a mean of 45%, 25% and 30% for stem, branch and leaf components, respectively.

Table 4-17: Repeated measures ANOVA of the effects of planting density on the proportions of biomass allocated to stem, branch and leaf components in *E. nitens*, *A. cordata* and *P. sitchensis*. Values in bold indicate significance at p ≤0.05.

Source of variation		*E. nitens*		*A. cordata*		*P. sitchensis*	
	df	F	P	F	p	F	p
Block	4	0.1	0.9718	0.2	0.9613	0.3	0.8837
Planting density	2	0.0	0.9864	0.0	1.0000	0.0	1.0000
Stem, Branch, Leaf	2	530.5	**<.0001**	160.6	**<.0001**	96.3	**<.0001**
Stem, Branch, Leaf x planting density	4	13.7	**<.0001**	6.8	**0.0008**	2.8	0.0499

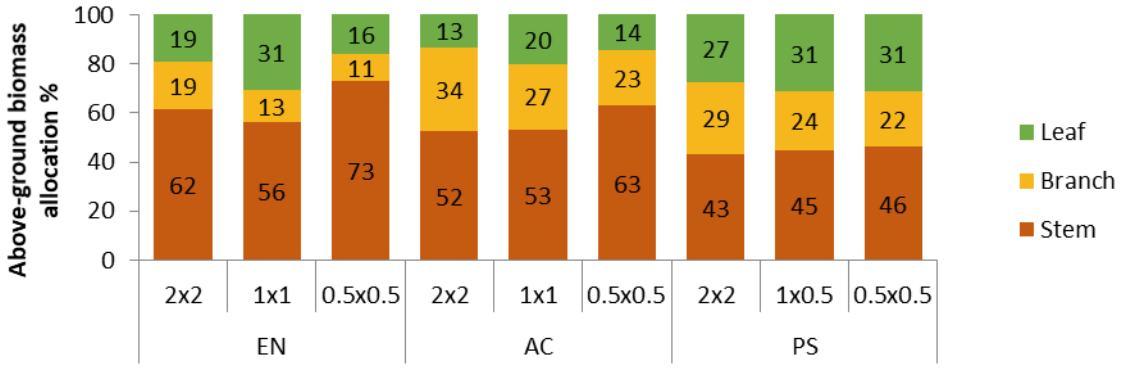

Figure 4-11: Proportion of biomass per tree (stem, branch and leaf) as a percentage of total biomass in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS) in response to planting density. Labels indicate percentage of total biomass of each tree component.

4.3.8 Wood density

Planting density had no effect on wood density (Eq. 13) in the three species (Table 4-18). Wood density differed between species (Figure 4-12) and was significantly higher ($p < 0.0001$) in *P. sitchensis* than in *A. cordata* or *E. nitens.* Wood density in *A. cordata* decreased significantly as stem height increased (measured at 20%, 40% and 60% of stem height). Wood density was significantly higher at 20% than at 40% of the tree height, with no significant difference being found between the 40% and 60% height positions in *P. sitchensis.* The opposite effect was observed for wood density in *E. nitens* with wood density increasing significantly with stem height. Mean wood densities were 433, 442 and 452 kg m^{-3} in *E. nitens*, 462, 451 and 439 kg m^{-3} in *A. cordata* and 484, 465, 455 kg m^{-3} in *P. sitchensis* at the 20%, 40% and 60% of stem height, respectively.

Table 4-18: Repeated measures ANOVA of basic density (dry weight / green volume) of 10 cm stem discs taken at 20%, 40% and 60% of the stem height for three species. Values in bold indicate significance at p ≤0.05.

Basic Density		*E. nitens*		*A. cordata*		*P. sitchensis*	
Total discs	df	F	p	F	P	F	p
Block	4	10.2	**0.0076**	3.0	0.0889	5.2	**0.0233**
Planting density	2	1.3	0.3500	0.8	0.4843	1.8	0.2296
Discs	2	5.7	**0.0112**	16.0	**<.0001**	8.8	**0.0013**
Discs x planting density	4	0.6	0.6958	2.9	**0.0450**	0.4	0.8372

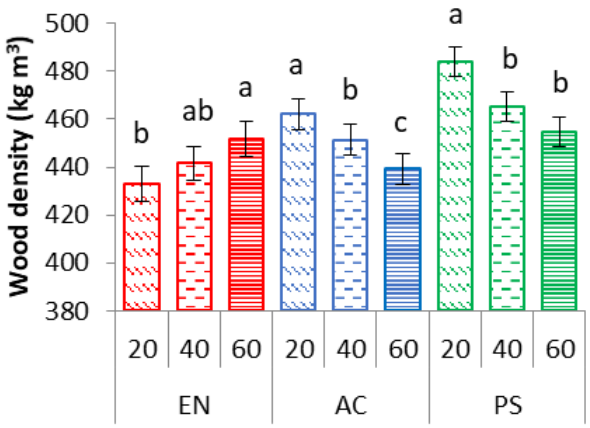

Figure 4-12: Mean basic wood density at 20%, 40% and 60% of height in *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS). Vertical lines = ± SE of the mean. Different letters indicate significant differences (p ≤0.05) with stem height, within species.

4.4 Discussion

Short rotation forestry seeks to make maximum use of all available growing space in as short a period as possible. The three species responded very differently to variations in planting density. Morphological and physiological effects of competition had manifested by year 4 in all species, well before differences in biomass allocation were detected. This indicates that planting density affected growth very early in development.

4.4.1 *E. nitens*

E. nitens was highly sensitive to competition stress during the 4 years of growth in the field. Crown size, as reflected by crown depth (percentage of the total tree height), tree height to branch length ratio and projected crown area, all declined in *E. nitens* as planting density increased. The smaller crown recorded for trees grown at the highest density may, in part, be attributed to the greater branch and leaf mortality in the lower crown, reducing crown depth. Height to the lowest live branch declined of *E. nitens* planted at wider spacings of 500 – 1667 stems ha^{-1} after 5 years growth in Tasmania (Neilsen and Gerrand, 1999). When leaves are unable to intercept sufficient light to maintain a positive carbon balance, the leaf and ultimately the branch dies (Forrester et al., 2010; Montagu et al., 2003). The carbon balance within a leaf is dependent on photosynthetic gains exceeding respirational losses (Flexas et al., 2006). The level of light at which this occurs varies with species (Givnish, 1988), but *E. nitens* would appear to be more sensitive to low light levels within the crown than *P. sitchensis or A. cordata*. Similar reductions in crown size in response to planting density were also found in the polytunnel experiment (Chapter 3). Although leaf morphology was generally not affected in the field trial, close spacing led to a decline in both chlorophyll concentration and photosynthesis rates in *E. nitens* foliage. Chlorophyll metabolism is known to be sensitive to stress (Knipling, 1970). An increase in planting density in *E. nitens* will reduce crown size and potentially limit its productive capacity as competition increases.

An important characteristic of wood used as biomass in SRF is its density. Planting density did not affect this characteristic in *E. nitens*. However, wood density increased with stem height, the opposite to that observed in *A. cordata* and

P. sitchensis. An increase in wood density with height is the general pattern found in eucalyptus (Bamber et al., 1969; Bhat et al., 2007; Quilhó and Pereira, 2001) and has been attributed to changes in fibre length. Fibre length decreases in wood and increases in the bark from base to tree top (Jorge et al., 2000).

A significantly greater proportion of photosynthate was allocated to stem biomass in *E. nitens* than in *A. cordata* or *P. sitchensis.* Although growth rates, biomass production and biomass allocation between tree components varied, treatment differences were difficult to detect in *E. nitens* because of the high degree of variation in growth, similar to the findings of other studies (Chapter 2.2.1). The high variability in growth reported for eucalyptus species was attributed to differences in soil condition in a Brazilian study (Campoe et al., 2012) whereas genetic factors were believed to have caused this response in a Tasmania study (Neilsen and Gerrand, 1999). However, the cause of variation in growth of *E. nitens* in this study could not be determined. A further issue of concern with *E. nitens* is its susceptibility to windthrow. Several storms resulted in windthrow of *E. nitens,* and although there was no root assessment done in the field trial, *E. nitens* had the smallest root: shoot ratio of the three species in the polytunnel experiment (Chapter 3) which may partly explain its susceptibility to windthrow.

4.4.2 *A. cordata*

A. cordata is a pioneer species that has a highly adaptable growth strategy (King, 1991). Of the three species studied, *A. cordata* altered stem architecture (by growing taller and thinner), more than branch or foliar architecture in response to changes in plant spacing. A high proportion of biomass was allocated to stem and branch elongation, but diameter growth was supressed as competition increased. The favouring of height growth at the expense of diameter growth is common among pioneer species, allowing them to out-compete competitors for light.

Crown volume, depth and spread remained almost constant in *A. cordata*, regardless of planting density. This resulted in *A. cordata* branches growing into the space of neighbouring trees, the opposite of that observed for *E. nitens* and *P. sitchensis* where branch length declined as planting density increased. *A. cordata* was the only species to fully occupy (i.e. its crown area covered the planting area to

which it was assigned) the 2×2 m planting area within 4 years. However, the above-ground biomass of *A. cordata* trees was similar to that of *P. sitchensis* trees and was significantly lower than in *E. nitens* at the end of the study. Trees tend to re-allocate biomass resources in response to competition from other trees, but overall production is often not affected (Poorter et al., 2012). Although above-ground biomass production rates per tree were not affected in *A. cordata* in this study, high stocking levels increased the quantity of biomass per unit area compared with low stocking levels.

Soil moisture content declined from August onwards and was significantly lower in the highest density plots of *A. cordata*. Three possible reasons can be advanced to explain the low soil water content at high planting density; 1) the higher LAI may have led to an increased canopy capture of rain water, much of which might have evaporated without entering the soil; 2) higher plot-level photosynthesis and transpiration rates resulting from a greater number of plants, and 3) higher moisture usage to maintain the cell turgor and the translocation of nutrients to a larger canopy per unit ground area (Figure 4-4). Water stress can reduce Ch_{leaf} (Schepers et al., 1996). However, planting density did not affect leaf chlorophyll concentration in *A. cordata*, suggesting that the lower moisture availability did not cause significant stress. Soil moisture content did not decline regardless of planting density, in plots of *E. nitens* or *P. sitchensis*.

4.4.3 *P. sitchensis*

P. sitchensis is regarded as a fast-growing species, but it grows relatively slowly during much of the juvenile period immediately after planting (Cannell, 1987). Initial spacing had no measurable impact on stem height or diameter, branch length or diameter values, crown depth or leaf nutrient levels (N, P, K) over the observed four years of growth. However, there was evidence that *P. sitchensis* was responding to competition due to spacing. Specific leaf area increased significantly as planting density increased, although no difference was found in needle area or dry mass. A greater proportion of biomass was allocated to leaf than branch components at a high density compared with low density planting. The higher stand biomass at high density planting can be attributed largely to the higher stem numbers rather than to differences in growth rate.

P. sitchensis produced higher density wood compared to *A. cordata* and *E. nitens* However, wood density declines in *P. sitchensis* with age from about 5 years onward before increasing again in the outer wood layer as mature wood is formed (Brazier, 1967). Slower growth rates are often associated with higher wood density (Brazier, 1977). Planting density did not affect the density of stem wood in *P. sitchensis*, at least during the 4-year period of development assessed in this study. In contrast, higher stocking resulted in an increase in wood density in *P. sitchensis* in older stands (40-50 years) in the UK (Brazier and Mobbs, 1993). The main focus of SRF systems is on biomass production. It is desirable to plant a species that has a high wood density as an SRF crop, but preferably this attribute should be combined with rapid growth and high productivity. The relatively high wood density, compared with the other species (Chapter 2.3.5), does not compensate for the low biomass yield, making *P. sitchensis* a less attractive species for SRF. A Washington provenance of *P. sitchensis* was used in the trial at Johnstown Castle. However, Oregon provenance is known to have good productivity in the southern parts of Ireland and may increase the yield under similar planting densities.

4.5 Conclusions

It was possible to identify early signs of competition before differences in growth rates could be detected in the three species. Planting density significantly affected crown size in *E. nitens*. Chlorophyll concentration declined as planting density increased in *E. nitens,* but photosynthesis rate was not affected. Although *E. nitens* underwent rapid growth during the four-year period of study, its growth rate was highly variable. Despite this variability, *E. nitens* produced greater stand-level quantities of biomass than *A. cordata* or *P. sitchensis,* particularly at high densities. Trees of *A. cordata* grew taller and thinner with long branches, occupying the available area quickly, especially at high density. Planting density did not affect chlorophyll concentration in *A. cordata*. However, photosynthesis rates declined in shade leaves as planting density increased *in A. cordata*, probably due to the dense canopy restricting light availability. Early competition effects were evident at leaf level in *P. sitchensis*, with those planted at highest density having the largest SLA. Although *P. sitchensis* was slower growing it

produced similar stand level biomass to *A. cordata* by the end of the 4-year observation period. This led to greater biomass allocation to stem components in *P. sitchensis* than in *A. cordata* and *E. nitens,* at the expense of branches. However, products from SRF generally favours a high wood-to-bark ratio and an increase in biomass allocation to stems, provided biomass quality is high with less bark and more wood, is a desirable characteristic.

4.6 Recommendations for future research

The assessments in this study were carried out only over a four-year period from the time of planting, which limits the practical applications of the findings. A continuation of these measurements over the full 15-year SRF period (or slightly longer) would provide information on the effects planting density on growth as competition increases. Data on the effects of planting density on root biomass would provide better information on biomass allocation patterns at the whole-tree level. Chlorophyll content measurements, which can be carried out quickly on a large number of trees, provides useful information on the response of trees to competition stress. Further research should be undertaken to determine target levels of Ch_{leaf} in lower crown leaves, which could then be used to inform decision-making in relation to planting density and other management aspects for the study species.

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5 Estimating productivity of short rotation forestry systems under Irish conditions

5.1 Abstract

It is difficult to determine the future productivity of potential short rotation forestry species in Ireland, mainly because too few data are available. Field trials have been established in an effort to specifically address this issue, but the trials are currently only four years old. Therefore, modelling tree growth may assist in predicting productivity of these species under such management systems. The 3-PG model was used in this study to predict growth and yield in shining gum (*Eucalyptus nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière). The aim of the study was to predict biomass production at various planting densities and estimate rotation lengths beyond the 4 years for which data were available from the field trial at Johnstown Castle. The model was populated with parameter values obtained from the Johnstown Castle field trial and (where appropriate data were not available) from relevant literature, along with climatic and environmental data for the site. The predicted growth was calibrated with data-sets of the same or similar species to ensure that the projections were reasonable. Biomass, leaf litterfall rate, specific leaf area, age of canopy cover and wood density values were adjusted to changes in planting density (2,500, 10,000, 20,000 and 40,000 stems ha^{-1}). The rotation length needed to maximise above- and below-ground biomass, mortality rates, and stand volume for each species were projected. Additional predictions were modelled using 15 years as a standard SRF rotation length to allow comparisons to be made. *E. nitens* productivity was projected to be substantially greater than that of *P. sitchensis* or *A. cordata* at all planting densities. The model predicted that *E. nitens* could produce *c.* 150 t above-ground woody biomass (AWB) ha^{-1} at 3,600 stems ha^{-1} on a 15-year rotation. Biomass yield was substantially lower in *A. cordata*, at 43 t AWB ha^{-1}, the lowest recorded for all three species and too low a yield to make it economically viable. *P. sitchensis* produced 85 t AWB ha^{-1} over a 15-year rotation. The slow initial growth rate and projected optimal rotation length of *c.* 35 years for *P. sitchensis* to maximise biomass production makes it an unsuitable species for biomass production.

5.1 Introduction

Purpose-grown tree crops to supply bioenergy production and fibre may play an important role in helping to increase carbon use efficiency, particularly where mild temperate climate conditions favour the growth of tree species, such as in Ireland. Newly-employed silvicultural approaches require the consideration of optimal planting density with estimates of the rotation length that a particular species will require and the final biomass yield that might be expected. This can be determined using data obtained from field trials. However, there are many permutations when combining species, spacings and rotation length. Therefore, the use of models to estimate biomass yield can provide essential information for decision making.

Modelling enables the representation of complex system interactions and behaviour in a simplified manner based on specific assumptions and conditions. The many potential combinations of abiotic and biotic disturbances, e.g. variation in climate and management, complicate the modelling of forest systems. Models can generate a likely growth response to a given scenario, e.g. estimate the impact of management decisions like establishment spacing. There are various approaches to modelling, but they generally fall into three categories: those based on empirical data, a process-based approach or a hybrid between both.

Empirical models represent the relationship between growth and yield based on specific data sets. Any potential impact of future climate change is not considered (Minunno et al., 2010), with the assumption that future conditions will be similar to those of the past (Garcia-Gonzalo et al., 2007). In contrast, process-based models estimate growth responses to environmental change. A process-based model can be applied beyond the spatial and temporal scope of empirical models (Mäkelä et al., 2000). Hybrid or scenario modelling combine the reliability of empirical relationships with the flexibility of process-based models (Mäkelä et al., 2000). Many model systems contain elements of both approaches and all models can be considered on an axis line between purely empirical at one end and totally process-based at the other (Korzukhin et al., 1996). The 3-PG model was used for estimating growth in this study.

The 3-PG process-based model produces stand-level forest growth estimations and was developed by Landsberg and Waring (1997). It was designed to project growth and development of even-aged stands, primarily in research applications (Sands and

Landsberg, 2002). The model is generic and, as such, is neither site nor species-specific (Sands, 2004), so therefore was considered the most appropriate for use in this study.

The aim of the study was to project biomass yield and productivity of shining gum (*E. nitens* (Deane & Maiden) Maiden), Italian alder (*Alnus cordata* (Loisel.) Duby) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière). Model projections require input of values either from observation of a particular trial or where this is not available, additional data may be obtained from the literature (Landsberg and Waring, 1997). The model was used to identify the optimum rotation length for maximising yield for each species. The model also allowed the simulation of the likely impact of a change in the Irish climate on growth and productivity. Modelling growth and development at various planting densities will provide information on some of the processes affecting productivity. The objectives of the study were to:

- estimate the impact of planting density on biomass yield in a SRF system;
- identify suitable rotation lengths for the three species in such a management system;
- investigate the sensitivity of the production system to climate change;
- assess the suitability of the study species for use in a SRF system in Ireland.

5.2 Materials and methods

5.2.1 Trial layout and site description

The 3-PG model was used to project the growth and development of three species in a spacing trial established at the Teagasc Environment Research Centre, Johnstown Castle, Co. Wexford (52°17'33.7" N, 6°31'42.4" W) in 2014, over a likely rotation of 15-20 years. The 3-ha site has a heavy gley soil at elevations ranging from 67 to 76 m above sea level and is 5.9 km from the coast. The site is prone to waterlogging (Chapter 4.2.1).

Seedlings of *Eucalyptus nitens, Alnus cordata* and *Picea sitchensis* were planted in June 2014 and established at four stocking densities – two of which were common to all species (0.5×0.5 m and 2×2 m) (Table 5-1). Each spacing treatment was replicated once per block for each species. Stand development of three planting densities was modelled for each species. Other spacings included in the trial were not included in the models (Chapter 4).

Table 5-1: List of species and descriptions of the material and treatments included in the spacing trial.

Species	Common name	Plant description†	Planting density (m)		Lines and rows	Stems ha^{-1}
E. nitens	Shining gum	1-year-old plugs	Low	0.5×0.5	4×4	40,000
			Medium	1×1	4×4	10,000
			High	2×2	5×5	2,500
A. cordata	Italian alder	2-year-old seedlings (2+0) bare roots	Low	0.5×0.5	4×4	40,000
			Medium	1×1	4×4	10,000
			High	2×2	5×5	2,500
P. sitchensis	Sitka spruce (Washington improved)	3-year-old transplant (2+1)	Low	0.5×0.5	4×4	40,000
			Medium	1×0.5	4×4	20,000
			High	2×2	4×3	2,500

† Plug plants (P) are seedlings grown in individual cells and transplanted with roots already bound in a plug of medium.
2+0 seedlings were grown for 2 year in a seed bed and were undercut
2+1 seedlings were grown for 2 years in a seed bed and 1 more year in a transplant bed

5.2.2 Model input data

This study utilised 3-PG$_{PJS}$ version 2.7 (Figure 5-1) and was applied using Microsoft Excel worksheets (Sands, 2010). The 3-PG model requires species data for parameterisation (Section 5.2.3) and calibration (Section 5.2.7). Figure 5-1 summarises the series of data inputs used to describe the growth conditions and generate growth projections. Site descriptive information from the Johnstown Castle spacing trial was used to initialise the model (Table 5-2). Climate data (Table 5-3) for the area was obtained from the Met Eireann synoptic station at Johnstown Castle (within 2 km of the trial site). These data included monthly mean minimum and maximum temperature, precipitation, frost days and incoming solar radiation from January 2014 to December 2018. Vapour pressure deficit (*VPD*) was calculated using the formula (Sands, 2010):

$$VPD = (SatVapPres\ at\ Tmax - SatVapPres\ at\ Tmin) \times 0.62 \qquad \text{(Eq. 14)}$$

where 0.62 = co-efficient adjustment for daytime *VPD; SatVapPres* = saturated vapour pressure, *Tmax* and *Tmin* = temperature maximum and temperature minimum (monthly), respectively. The number of frost days was calculated as the total number of days when minimum air temperatures were <0˚C. The available soil water (ASW) was estimated by adjusting the value until it ceased to affect the model output (Sands, 2004) which was 190 mm in this study.

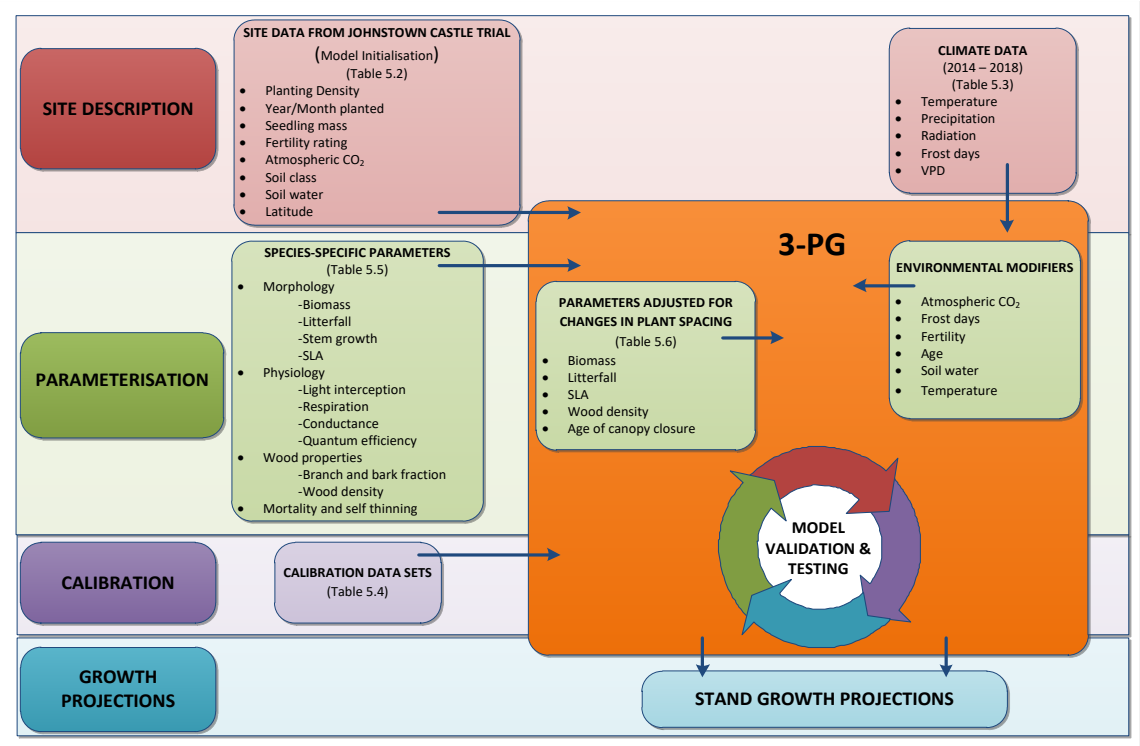

Figure 5-1: A schematic diagram indicating the data inputs required for the various processes within the 3-PG model system.

Table 5-2: A summary of stand values and site factors for initialisation of the 3-PG model for use at the Johnstown Castle site.

Stand initialisation and site factor data			
Month planted =	June	**Latitude =**	52.3° North
Initial age =	0	**Atmospheric CO_2 =**	403 ppm
End age =	50 years	**Soil class =**	C
Seedling mass =	1 g seedling^{-1}	**Initial Available soil water (ASW) =**	190 mm
Year planted =	2014	**Minimum ASW =**	190 mm
Fertility rating =	1	**Maximum ASW =**	190 mm
Initial stocking =	Varied as required		

Table 5-3: Mean monthly climate data for years 2014 - 2018, sourced from the Met Eireann synoptic station at Johnstown Castle.

Month	T_{max} (°C)	T_{min} (°C)	Rain (mm)	Solar radiation ($MJ^{-1}m^2$)	Frost days	VPD (mBar)
January	12.16	-0.82	107.66	2.60	12.00	4.21
February	12.48	-1.06	90.18	5.47	15.00	4.41
March	13.72	-0.52	91.94	8.43	9.00	4.91
April	15.14	1.18	62.10	13.72	1.00	5.28
May	19.68	4.12	75.94	17.57	0.00	7.36
June	22.46	6.84	60.24	20.65	0.00	8.64
July	22.72	8.54	61.76	18.49	0.00	8.25
August	21.60	8.10	73.70	14.63	0.00	7.50
September	19.66	6.60	86.58	11.07	0.00	6.57
October	16.98	4.04	95.76	6.11	0.00	5.60
November	14.10	0.62	116.06	3.11	3.00	4.85
December	12.46	0.06	142.66	1.84	6.00	4.16

5.2.3 Parameterisation

Parameterisation is best achieved using direct measurements (stand-level data) or by comparison with other species where such information is more widely available (Sands, 2004). Where possible the model parameterisation values for each species were obtained from the Johnstown Castle trial or from published literature (Table 5-4). Otherwise parameter values were estimated or default values from Sands and Landsberg (2002) were used. Model functioning was particularly sensitive to some parameter values, which had a high impact on the modelled output. Therefore, the partitioning of biomass between foliage and stem; litterfall rates; stem biomass to stem diameter relationship; age of canopy closure; mortality and self-thinning parameters used default values from literature (Section 5.2.7) for each species and planting density.

Growth characteristics affected by planting density were identified from the field data. These data then were used as parameter values (stem mass v. diameter allometric relationship; specific leaf area at age 0; specific leaf area for mature leaves; and minimum basic wood density for young trees) specific to the planting densities in the trial (Table 5-5).

Specific leaf area (SLA) values (Table 5-4) are dependent on stand age (Sands, 2004) but are also affected by planting density. Specific leaf area values of young trees

were obtained from observations made in the polytunnel experiment (Chapter 3). The SLA data from more mature trees were obtained from the Johnstown Castle trial for *E. nitens* and *A. cordata* (Chapter 4). No SLA data were available for leaves of fully mature trees for these species growing under Irish conditions. The values for needles from mature trees for *P. sitchensis* were obtained from Irish data (Tobin et al., 2006) and the SLA for young needles were based on the data obtained from the Johnstown Castle trial (Chapter 4).

Canopy closure is a gradual process. As trees grow in a stand the branches from neighbouring trees begin to overlap and compete for light and other resources (Tabbush and White, 1988). The parameter values for the age at which canopy closure has occurred (fullCanAge) were estimated for each species and spacing, based on the projected crown area data obtained in the field trial at Johnstown Castle (Chapter 4.3). The parameter values for the age of canopy closure used in the model were estimated for *E. nitens* to be 7, 5 and 4 years for low, medium and high planting density, respectively; for *A. cordata* 5, 4, and 3 respectively, and for *P. sitchensis* 10, 7 and 5 respectively.

There are six growth modifiers in the 3-PG model (Figure 5-1) which account for environmental effects on productivity (Sands, 2004). Most modifier values were obtained from published literature (Table 5-4). Soil modifier values were determined from soil texture tables in Landsberg and Waring (1997). The soil at the trial site was predominately clay, therefore the appropriate parameters for the moisture deficit ratio were, c_Θ 0.4 (constant) and n_Θ 3 (power) (Sands, 2010). Fertility modifier values range between 0 (highly infertile) to 1 (highly fertile) (Landsberg and Waring, 1997). As there are no data on root biomass or root turnover rates the effects of fertility rating cannot be separated from canopy quantum efficiency and therefore was set to FR=1 in stand initialisation (Sands and Landsberg, 2002). Since the objective of the projections concerned the impacts of different planting densities on the growth of each species, nutrient availability was assumed non-limiting and the fertility nutrient value (FR) was set to 0.5, as recommended by Landsberg et al. (2003).

Stem mortality in the 3-PG model begins when the mean tree stem mass (w_s) reaches a maximum stem mass per tree at 1,000 trees ha^{-1} (w_{sx1000}). The 3-PG sub-models do not project mortality rates for young stands, so the mortality rate tends to

have a sudden impact and cause a rapid decline once W_s exceeds W_{sx1000}. Therefore, this is an artefact of the 3-PG system and may not be a true projection of mortality.

5.2.4 Growth projections

Projections were run with the 3-PG model using one data-set of parameterised values per planting density per species. In conventional forestry systems the rotation length (RL) for a species can be determined by using the age where mean annual increment (MAI) and current annual increment (CAI) curves intersect (Goundrey, 1960). Harvesting at this rotation length allows the production of maximum sustainable volume (Burley et al., 2004; Smith et al., 1997). Model projections of total above-ground woody biomass (-foliage) (AWB) at RL were used to compare species productivity at different spacings. In addition, modelled output at a standardised rotation of 15 years was used to examine the stand productivity in a SRF context. Although the target rotation period examined was between 15-20 years, the end date for the projections was 50 years.

5.2.5 Alternative stocking projections

Practical limitations constrained the number of initial planting densities in the field trial, thus limiting model development options. The model was used to estimate productivity for a series of planting densities over a standardised 15-year rotation (RL_{15}). The first estimate was based on a planting density of 1,600 stems ha^{-1} arising from a square spacing of 2.5 × 2.5 m. The spacing was decreased in steps of 20 cm (resulting in square spacings of 2, 1.8, 1.6, 1.4, 1.2, 1, 0.8 m) and the model projections were rerun until a stocking density resulted in a reduction in stand biomass output. Estimations of stocking $level_{RL}$, AWB and stand volume were obtained. The parameter values for 2,500 stems ha^{-1} for each species (Table 5-4) were used as the basis for the series of model runs.

Table 5-4: Summary of values used to parameterise the 3-PG model for *E. nitens, A. cordata* and *P. sitchensis*. Values are listed as site or species-specific, along with the sensitivity of the parameter: low (L), medium (M) or high (H) (Sands, 2004). The data source used is indicated as: directly observed (O) from Johnstown Castle field trial (Chapter 4) or Kinsealy experiment (Chapter 3); obtained from generic values based on prior knowledge - default (D); from published literature (L); or estimated (E) by adjusting a parameter value to obtain best fit with observed time-series data output (during calibration). Superscripted letters indicate the source.

Parameters	Name	Units	*E. nitens*	*A. cordata*	*P. sitchensis*	Species or site specific (Sensitivity)	Data origin
Biomass partitioning and turnover							
Allometric relationships & partitioning							
Foliage: stem partitioning ratio @ D=2 cm	pFS_2	-	0.381	0.301	[1]0.860	Species (H)	O/O/L
Foliage: stem partitioning ratio @ D=20 cm	pFS_{20}	-	[2]0.089	0.09	0.85	Species (H)	L/E/ E
Constant in the stem mass v. diam. Relationship	α_S	-	[2]0.098	0.029	0.215	Species (M)	L/O/O
Power in the stem mass v. diam. Relationship	n_S	-	[2]2.222	2.336	2.628	Species (H)	L/O/O
Maximum fraction of NPP to roots	pRx	-	[3]0.8	[3]0.8	[1]0.401	Species (M)	D/D/L
Minimum fraction of NPP to roots	pRn	-	[4]0.1	[3]0.25	[1]0.18	Species (M)	D/L/L
Litterfall & root turnover							
Maximum litterfall rate	gammaFx	1/month	0.018	0.016	0.063	Both (H)	E
Litterfall rate at t = 0	gammaF0	1/month	[3]0.001	[3]0.001	[3]0.001	Both (L)	L
Age at which litterfall rate has median value	tgammaF	months	12	12	36	Both (L)	E
Mean monthly root turnover rate	gammaR	1/month	[3]0.015	[3]0.015	[5]0.017	Both (L)	L
NPP & conductance modifiers							
Temperature modifier (fT)							
Minimum temperature for growth	T_{min}	deg. C	[2]2	[9]-6	[5]-5	Species (L)	L
Optimum temperature for growth	T_{opt}	deg. C	[2]13	[3]16	[5]15	Species (M)	L
Maximum temperature for growth	T_{max}	deg. C	[2]32	[3]40	[5]35	Species (L)	L
Frost modifier (fFRost)							
Days production lost per frost day	kF	days	[5]1	[5]1	[5]1	Species (L)	L
Soil water modifier (fSW)							
Moisture ratio deficit for $f_q = 0.5$	SW_{const}	-	0.4	0.4	0.4	Site (H)	O
Power of moisture ratio deficit	SW_{power}	-	3	3	3	Site (L)	O
Atmospheric CO_2 modifier (fCO_2)							
Assimilation enhancement factor at 700 ppm	$fCalpha_{700}$	-	[3]1.4	[3]1.4	[3]1.4		D
Canopy conductance enhancement factor at 700 ppm	fCg_{700}	-	[3]0.7	[3]0.7	[3]0.7		D

Parameters	Name	Units	*E. nitens*	*A. cordata*	*P. sitchensis*	Species or site specific (Sensitivity)	Data origin
Fertility effects							
Value of (m) when FR = 0	m0	-	[7]0	[7]0	[7]0	Species (L)	L
Value of 'fNutr' when FR = 0	fN0	-	[7]0.5	[7]0.5	[7]0.5	Species (M)	L
Power of (1-FR) in 'fNutr'	fNn	-	[7]1	[7]1	[7]1	Species (L)	
Age modifier (fAge)							
Maximum stand age used in age modifier	Max_{Age}	years	50	50	50	Species (L)	E
Power of relative age in function for fAge	n_{Age}	-	[8]4	[8]4	[8]4	Species (L)	L
Relative age to give fAge = 0.5	r_{Age}	-	[8]0.99	[8]0.99	[8]0.99	Species (L)	L
Stem mortality & self-thinning							
Mortality rate for large t	gammaNx	%/year	[11]0.6	1	1	Site	L/D/D
Seedling mortality rate (t = 0)	gammaN0	%/year	[11]0.25	0.1	0.1	Site	L/D/D
Age at which mortality rate has median value	tgammaN	years	[11]9	1	1	Site	L/D/D
Shape of mortality response	ngammaN	-	[11]1	1	1	Species	L/D/D
Max. stem mass per tree @ 1,000 trees ha^{-1}	W_{Sx1000}	kg/tree	[11]285	[10]180	[1]291	Both (L)	L
Power in self-thinning rule	$thin_{Power}$	-	[5]1.5	[5]1.5	[5]1.5	Species (L)	D
Fraction mean single-tree foliage biomass lost per dead tree	m_F	-	[11]0.32	[3]0	[5]0.5	Species (L)	L
Fraction mean single-tree root biomass lost per dead tree	m_R	-	[11]0.32	[3]0.2	[5]0.3	Species (L)	L
Fraction mean single-tree stem biomass lost per dead tree	m_S	-	[11]0.32	[3]0.2	[5]0.2	Species (L)	L
Canopy structure and processes							
Specific leaf area							
Specific leaf area at age 0	SLA_0	m^2/kg	12.93	18.12	5.94	Species (L)	O
Specific leaf area for mature leaves	SLA_1	m^2/kg	7.51	12.79	[1]4.48	Species (H)	O/O/L
	tSLA	years				Species (L)	O
Age at which specific leaf area = $(SLA_0+SLA_1)/2$			2.4	2.4	24.5		
Light interception							
Extinction coefficient for absorption of PAR by canopy	k	-	[3]0.5	[3]0.5	[3]0.5	Species (M)	D
Age at canopy cover	FullCanAge	years	7	5	10	Both (M)	E
Maximum proportion of rainfall evaporated from canopy	MaxIntcptn	-	[11]0.32	[5]0.15	[5]0.15	Species (M)	L
LAI for maximum rainfall interception	LAImaxIntcptn	-	[11]2	2	[5]5	Species (L)	L/E/L
Production and respiration							
Canopy quantum efficiency	alpha	molC/molPAR	[8]0.03	0.015	[8]0.03	Species (H)	L/E/L
Ratio NPP/GPP	Y	-	[5]0.47	[5]0.47	[5]0.47	Species (H)	L

Parameters	Name	Units	*E. nitens*	*A. cordata*	*P. sitchensis*	Species or site specific (Sensitivity)	Data origin
Conductance							
Minimum canopy conductance	MinCond	m/s	[3]0	[3]0	[3]0	Species (L)	L
Maximum canopy conductance	MaxCond	m/s	[3]0.02	[3]0.02	[3]0.02	Species (H)	L
LAI for maximum canopy conductance	LAIgcx	-	[12]3.33	[12]3.33	[12]3.33	Species (L)	L
Defines stomatal response to VPD	CoeffCond	1/mBar	[3]0.05	[3]0.05	[3]0.05	Species (L)	L
Canopy boundary layer conductance	BLcond	m/s	[3]0.2	[3]0.2	[3]0.2	Both (L)	L
Wood and stand properties							
Branch and bark fraction ($frac_{BB}$)							
Branch and bark fraction at age 0	$frac_{BB0}$	-	[2]0.65	[3]0.75	[5]0.15	Species (L)	L
Branch and bark fraction for mature stands	$frac_{BB1}$	-	[2]0.1	[3]0.15	[5]0.15	Species (L)	L
Age at which $frac_{BB}$ = ($frac_{BB0}$+$frac_{BB1}$)/2	tBB	years	[2]2	[3]2	[5]1.5	Species (L)	L
Basic Density							
Minimum basic density - for young trees	rho_{Min}	t/m^3	0.442	0.451	0.47	Both (H)	O
Maximum basic density - for older trees	rho_{Max}	t/m^3	[13]0.417	[13]0.354	[14]0.34	Both (H)	L/L/L
Age at which rho = (rho_{Min}+rho_{Max})/2	tRho	years	4.5	4.5	26	Both (M)	
Stem height							
Constant in the stem height relationship	aH	-	0	0	0.0907	Species	-/-/L
Power of DBH in the stem height relationship	nHB	-	0	0	1.4344	Species	-/-/L
Power of stocking in the stem height relationship	nHN	-	0	0	0.0949	Species	-/-/L
Stem volume							
Constant in the stem volume relationship	aV	-	[2]0.00002	0	0	Species	L/-/-
Power of DBH in the stem volume relationship	nVB	-	[2]2.484	0	0	Species	L/-/-
Power of stocking in the stem volume relationship	nVN	-	[2]1.31	0	0	Species	L/-/-
Conversion factors							
Intercept of net v. solar radiation relationship	Qa	W/m^2	-90	-90	-90		D
Slope of net v. solar radiation relationship	Qb	-	0.8	0.8	0.8		D
Molecular weight of dry matter	gDM_mol	gDM/mol	24	24	24		D
Conversion of solar radiation to PAR	molPAR_MJ	mol/MJ	2.3	2.3	2.3		D

[1] (Tobin et al., 2006); [2] (González-García et al., 2015); [3] (Sands and Landsberg, 2002); [4] (Resh et al., 2003); [5] (Waring, 2000); [6] (Turner et al., 1976); [7] (Landsberg et al., 2003); [8] (Landsberg and Waring, 1997); [9] (Claessens et al., 2010); [10] (Potithep and Yasuoka, 2011); [11] (Pérez-Cruzado et al., 2011); [12] (Sands, 2010); [13] (Senelwa and Sims, 1999); [14] (Petty et al., 1990).

Table 5-5: The list of parameter values that were altered to model changes in stocking density (2,500, 10,000, 20,000 and 40,000 stems per ha^{-1}) for *E. nitens, A. cordata* and *P. sitchensis*. The data sources used is indicated as: directly observed (O) from Johnstown Castle field trial (Chapter 4) or Kinsealy trial (Chapter 3); from published literature (L); or estimated (E) by adjusting a parameter value to obtain best fit with observed time-series data output.

Parameters	Name	Units	*E. nitens*	*A. cordata*	*P. sitchensis*	Data origin
Stems per ha^{-1}			**2,500/20,000/40,000**	**2,500/20,000/40,000**	**2,500/10,000/40,000**	
Biomass partitioning and turnover						
Constant in the stem mass v. diam. Relationship	aS	-	0.018/0.022/0.014	0.006/0.006/0.006	0.022/0.023/0.029	O
Power in the stem mass v. diam. Relationship	nS	-	2.659/2.551/3.096	3.646/3.646/3.646	2.628/2.589/2.439	O
Litterfall & root turnover						
Maximum litterfall rate	gammaFx	1/month	0.022/0.028/0.03	0.016/0.016/0.016	0.063/0.063/0.063	E
Specific leaf area						
Specific leaf area at age 0	SLA_0	m^2/kg	12.93/12.93/12.93	18.12/18.12/18.12	5.936/6.583/8.532	O
Specific leaf area for mature leaves	SLA_1	m^2/kg	7.507/7.507/7.507	11.57/13.31/13.49	[1]4.48/[1]4.48/[1]4.48	O/O/L
Light interception						
Age at canopy cover	fullCanAge	Years	7/5/4	6/4/3	10/7/5	E
Basic Density						
Minimum basic density - for young trees	rhoMin	t/m^3	0.440/0.452/0.433	0.459/0.453/0.441	0.478/0.458/0.467	O

[1] (Tobin et al., 2006)

5.2.6 Impact of future climate

To investigate the likely impact of future climate change on stand biomass yield, simulated temperature and precipitation data were used in the model instead of the current climate data. Estimates, representing a best and worst case scenario for climate change likely to affect Ireland for the period 2021 – 2050, were obtained from the Environmental Protection Agency report through the representative concentration pathways (RCP): RCP2.6 and RCP8.5 (Table 5-6) (Fealy et al., 2018). The available soil water (ASW) value used in the site description was changed to 150 mm (instead of 190 mm), and the model growth projections were re-run with the simulated climate information.

Table 5-6: Projected changes in temperature (°C) and precipitation (% change) were sourced for the periods 2021–2050 from RCP2.6 and RCP8.5 scenarios from climate simulations (Fealy et al., 2018).

Season	Temperature (°C) 2021–2050		Precipitation (% change) 2021–2050	
	RCP2.6	RCP8.5	RCP2.6	RCP8.5
Winter (December to February)	0.8	1.0	–1.8	–2.3
Spring (March to May)	0.3	0.7	7.6	0.2
Summer (June to August)	0.8	1.2	–13.6	–6.4
Autumn (September to November)	0.8	1.5	0.9	–1.3

5.2.7 Model calibration

Model outputs were compared with calibration data sets from published sources (Table 5-7). Calibration involved comparing model output for components such as stem biomass, leaf area index, DBH and stand volume with calibration data. The parameter values that were adjusted or fitted using the calibration data (Table 5-8) are listed in Table 5-4 (see data origin column). Checks were made to ensure that any adjusted parameter values (Table 5-4) remained reasonable (biologically possible) and realistic, as indicated by Sands (2010). A comparison between observed and projected diameter and stand volume for each species was carried out (Figure 5-2) to check that calibration was adequate. The data used for model calibration (Table 5-7, Table 5-8) were sourced from very diverse origins. The data characterising *P. sitchensis* stand development was most suitable since it came from research sites on similar soil types and climatic conditions. However, due to a dearth of data pertaining to *E. nitens* and

A. cordata in Ireland, the information gaps were filled from the most appropriate sources available.

An assessment of a model's validity requires a separate validation data set that is independent of the model-fitting data to simulate the time-course of stand growth (Amaro et al., 2003). The model projections were not validated in this study because of a lack of suitable data.

Table 5-7: Data sets were obtained to describe the change in growth characteristics with time for the three trial species. These were used to calibrate the model.

Species	Source	Growth characteristics	Site location	Stand age	Study details
E. nitens	(González-García et al., 2016)	LAI	N. Spain	4-6	Chronosequence, 5 sites Range of soil types, pH <5.3 Elevation 450 to 700 m
	(Pinkard and Neilsen, 2003)	DBH, stand volume	Tasmania	7	Periodic observation, 1 site Site details not available
	(Neilan and Thompson, 2008)	Stem height, stem diameter	Ireland	9-23	Chronosequence, 6 sites Counties: Sligo, Tipperary, Wexford, Waterford, Cork Site details not available
	(Thompson et al., 2012)	Stem height, stem diameter, volume	Ireland	16-28	Chronosequenced 5 sites Counties: Tipperary, Waterford, Wexford, Wicklow Site details not available
A. cordata	(Leslie et al., 2017)	Stem height, stem diameter, volume,	Cumbria, UK	2-3	Periodic observation, 1 site *Alnus glutinosa* Soil: clay loam brown earth, pH 6.0 Elevation 160 m
	In: (Claessens et al., 2010) Exerpts from: -(Sopp, 1974) -(Schober, 1995) -(Locklow, 1994)	Stem height, volume	 Hungary, Germany Germany	 5 25 15	 Yield tables Yield tables Yield tables
	(Tobin et al., 2014)	Stem height, stem diameter	Ireland	6-12	Chronosequence, 3 sites Alnus glutinosa Soil: gley Elevation 250m
	(Townsend and Douglass, 1994)	Stem height	USA	7	Periodic measurement Soil: silt loam
	(Trappe et al., 1968)	Stem height, stem diameter, volume,	Canada	10-30	Summary data of 122 sites *Alnus rubra*
	(Turner et al., 1976)	Stem height, stem diameter, stand dry mass	USA	43-44	Periodic measurement *Alnus rubra* Soil mineral, pH 5.1
P. sitchensis	(Tobin et al., 2006)	Stem height, stem diameter, volume, stand dry mass, LAI	Ireland	7-46	Chronosequence, 6 sites County Laois Soil: Gley Elevation 160 to 280 m

Table 5-8: Time-series data used to calibrate parameters.

Stand age	Height (m)	DBH (cm)	Vol ($m^3 ha^{-1}$)	LAI	Ref
		E. nitens			
4		11.6		4.2	(González-García et al., 2016)
4		9.7		3.2	(González-García et al., 2016)
6		6.2		3.7	(González-García et al., 2016)
7				4.1	(González-García et al., 2016)
7				3.4	(González-García et al., 2016)
7		20	227		(Pinkard and Neilsen, 2003)
7		18.5			(Pinkard and Neilsen, 2003)
4				2.8	(González-García et al., 2016)
9	15.7				(Neilan and Thompson, 2008)
13	21.5	26			(Neilan and Thompson, 2008)
13	22.5	26			(Neilan and Thompson, 2008)
13	17	16			(Neilan and Thompson, 2008)
13	20	24			(Neilan and Thompson, 2008)
14	22.2				(Neilan and Thompson, 2008)
16		24.2	418	26.1	(Thompson et al., 2012)
17	22.75	19.9	543.9	32	(Thompson et al., 2012)
17	25	22	445	26.2	(Thompson et al., 2012)
17	23.79	20.6	482.9	28.4	(Thompson et al., 2012)
18	26				(Neilan and Thompson, 2008)
23	31.1				(Neilan and Thompson, 2008)
28	32	29	656	23.4	(Thompson et al., 2012)
		A. cordata			
2	1.6	2.87	9.6		(Leslie et al., 2017)
3	1.9	4.38	23		(Leslie et al., 2017)
5	8		50		(Claessens et al., 2010)
6	3.9	6.07			(Tobin et al., 2014)
7	3.6				(Townsend and Douglass, 1994)
10	16.8	9.1	59.5		(Trappe et al., 1968)
12	10.5	7			(Tobin et al., 2014)
15	12.2		60		(Claessens et al., 2010)
20	23.2	17	99		(Trappe et al., 1968)
24	16.2	15.5			(Turner et al., 1976)
25	25.9	20	117.5		(Trappe et al., 1968)
25	17.3		154		(Claessens et al., 2010)
30	28	23.6	135.5		(Trappe et al., 1968)
40	21		228		(Schober, 1995)
44	22.4	19.5			(Turner et al., 1976)
		P. sitchensis			
5	1.6	3.36		0.43	(Tobin et al., 2006)
7	4	6			"
9		5.6	16.5		"
14	8	12.7	116.8		"
14		15.8	248.6		"
19	14	25		5	"
21	16	21.7	288.1		"
30	18	24.2	632.4		"
45	30	32.2	869.9		"

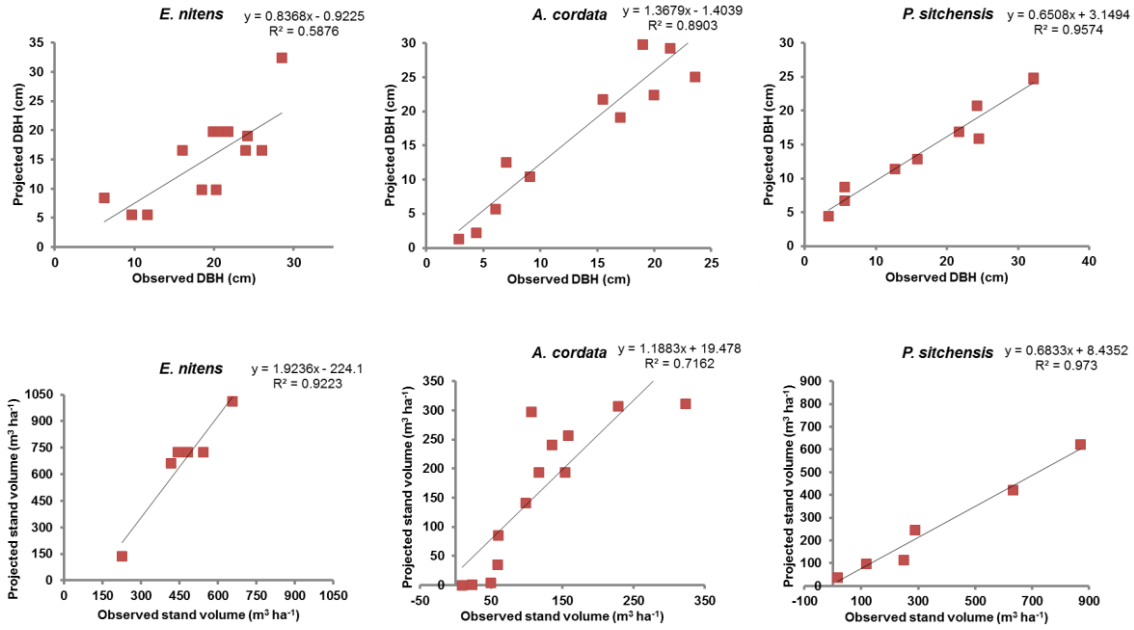

Figure 5-2: Calibration check with observed and projected net change in diameter at breast height (DBH) and stand volume in *E. nitens, A. cordata* and *P. sitchensis*. Data shows linear regression equations (y) and coefficient of determination (R^2).

5.3 Results

Stand level projections made using 3-PG are presented for *E. nitens, A. cordata* and *P. sitchensis* over a 50-year time frame for the three planting densities. The projected rotation length varied with species and to a lesser degree with planting density. The rotation length for each species depicted was rounded up to show ± 5 years after its maximum rotation length. The sudden drop observed in the CAI (Figures 5-4, 5-6 and 5-8) may be an artefact of the 3-PG mortality sub-model.

5.3.1 *E. nitens*

The amount of above-ground woody biomass (AWB), root and foliage biomass were projected to be lower for trees at the low planting density in *E. nitens.* However, by year 20 the biomass production rate at the low planting density was predicted to exceed that achieved at the medium and high densities (Figure 5-3). AWB, root and foliage accumulation rates were similar for the medium and high planting density.

Mortality increased at the high planting density from year 7 onward, and from year 11 onwards at the medium planting density. The stocking levels were projected to decline to 2,298, 3,275, 3,651 stems ha^{-1} by year 20, which represented 8, 67 and 91% tree mortality at low, medium and high planting densities, respectively.

Stand volume at 2×2 m spacing continued to increase beyond year 20 according to the model. At the medium spacing, stand volume increased until year 10 when the rate of increase slowed considerably. A high mortality rate affected stand volume at the high planting density, which resulted in a maximum stand volume of 610 m^3 ha^{-1}, followed by a slow decline thereafter. The mean annual increment increased until mortality rates caused it to decline for all planting densities.

The rotation length (RL) differed for each planting density, from 20 years for 2,500 stems ha^{-1} to 11 years for 10,000 stems ha^{-1} and 7 years for the 40,000 stem ha^{-1} (Figure 5-4). Therefore, the rotation length for the medium and high planting density was projected to occur several years before the selected age of 15 years for SRF. Tree mortality was estimated at 8%, 9% and 24% at the low, medium and high planting densities, respectively, at the end of the rotations (mentioned above) (Table 5-9). The

medium spacing was projected to produce higher above-ground woody biomass than the low planting density at 15 years.

Table 5-9: Model projections of growth at three planting densities for *E. nitens*. Rotation length (RL) was defined as the point at which the MAI and CAI curves intersected (Figure 5-4). Biomass and volume production were estimated over this period. Biomass production over a standardised period of 15 years was also estimated.

Planting density	MAI_{RL} (m^3 ha^{-1} yr^{-1})	$Stocking_{RL}$ (ha^{-1})	RL	Basal $area_{RL}$ (m^2 ha^{-1})	AWB_{RL} (t ha^{-1})	Root $biomass_{RL}$ (t ha^{-1})	Stand $volume_{RL}$ (m^3 ha^{-1})	AWB_{15} (t ha^{-1})
2×2 m (2,500)	55.136	2,298	20	100.161	180.838	10.685	1,102.692	122.177
1×1 m (10,000)	93.752	9,107	11	88.022	94.441	9.215	1,031.273	124.197
0.5×0.5 m (40,000)	87.162	30,272	7	54.020	51.799	7.055	610.136	113.533

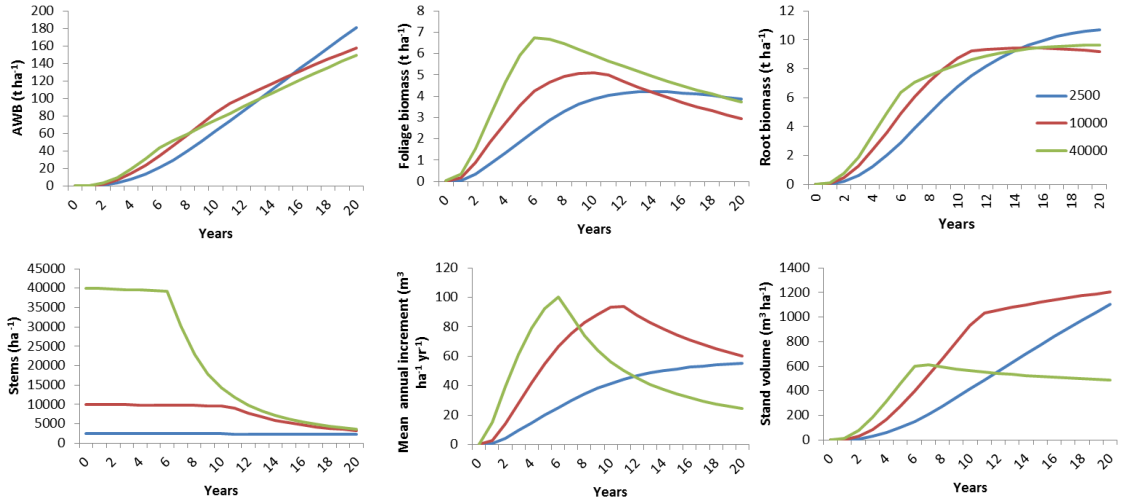

Figure 5-3: Model projections of stand development at three planting densities of above-ground woody biomass, foliage and root biomass; and stem mortality, mean annual increment and stand volume in *E. nitens*.

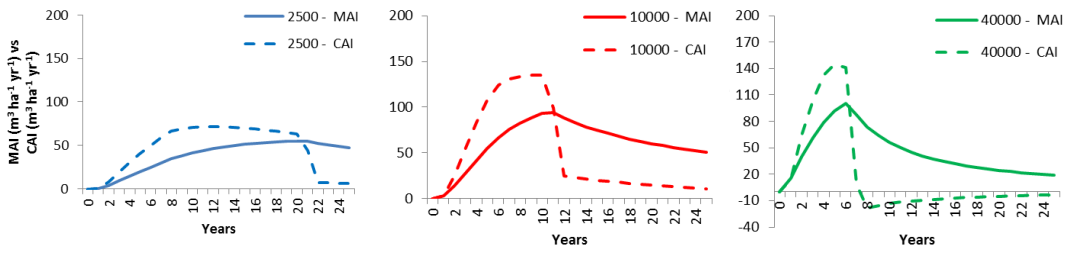

Figure 5-4: Mean annual volume increment (MAI) with mean current annual volume increment (CAI) for *E. nitens*.

5.3.2 *A. cordata*

AWB, root and foliage biomass accumulation were predicted to be lower at the 2×2 m spacing than the two higher planting densities in *A. cordata* (Figure 5-5). AWB for the two higher planting densities remained similar throughout the projected period. Stem mortality increased from year 8 at the high stocking rate and from year 16 onwards at the medium stocking rate. At the end of the 40-year projections, mortality was 32, 83 and 96% at low, medium and high planting densities, respectively. The mortality rate at low stocking resulted in a loss of <800 stems by the end of the projection period. The predicted stocking levels by year 40 were 1,697, 1,679 and 1,682 stems ha^{-1}, at the low, medium and high densities, respectively.

The projected MAI at the two highest planting densities increased to within 8 m^3 ha^{-1} of each other by year 14 (Figure 5-5). Similarly, stand volume at the two higher planting densities were similar by year 14 with less than 2 m^3 ha^{-1} between them. The MAI and stand volume were lowest at the low planting density compared to the other two densities throughout the projection period.

The rotation length (RL) was estimated at 35, 24 and 26 years for low, medium and high planting densities, respectively in *A. cordata* (Table 5-10). The difference in RL between the low and higher planting densities was >9 years, resulting in a large fall in AWB_{RL} and stand $volume_{RL}$ as stocking increased. The MAI for all planting densities at their respective RL was similar. Considering the above-ground woody biomass production during a standardised 15-year rotation (AWB_{15}), productivity was greatest at the medium and high stocking densities.

Table 5-10: Model projections of growth at three planting densities for *A. cordata*. Rotation length (RL) was defined as the point at which the MAI and CAI curves intersected (Figure 5-6). Biomass and volume production were estimated over this period. Biomass production over a standardised period of 15 years was also estimated.

Planting density	MAI_{RL} (m^3 ha^{-1} yr^{-1})	$Stocking_{RL}$ (ha^{-1})	RL	$Basal\ area_{RL}$ (m^2 ha^{-1})	AWB_{RL} (t ha^{-1})	$Root\ biomass_{RL}$ (t ha^{-1})	$Stand\ volume_{RL}$ (m^3 ha^{-1})	AWB_{15} (t ha^{-1})
2×2 m (2,500)	8.023	1,784	35	23.684	117.099	13.113	280.791	29.880
1×1 m (10,000)	8.821	4,110	24	29.658	88.787	14.522	211.691	50.637
0.5×0.5 m (40,000)	8.797	3,539	26	28.882	95.689	14.655	228.722	52.231

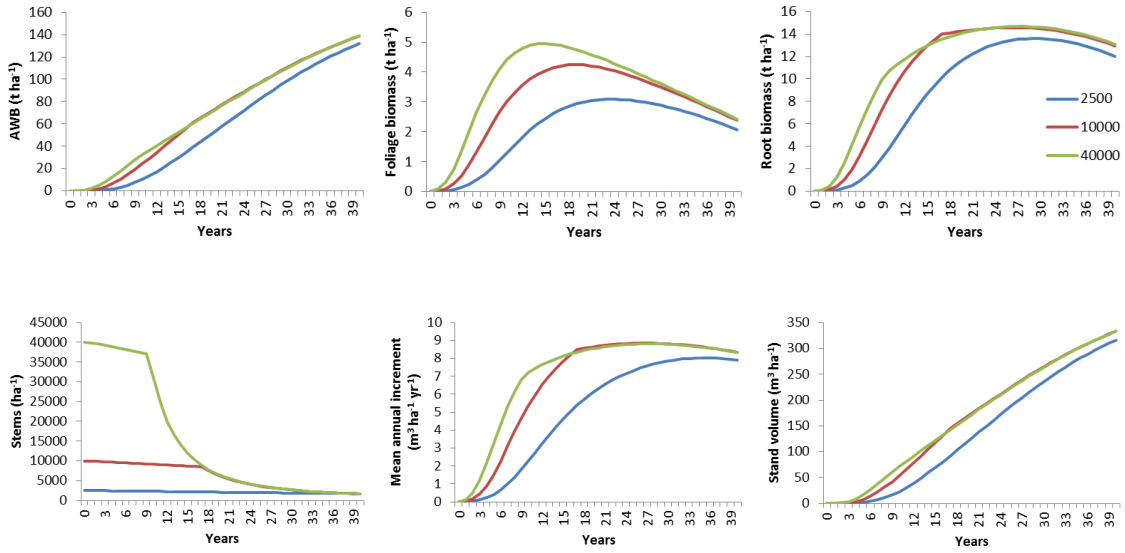

Figure 5-5: Model projections of stand development at three planting densities of above-ground woody biomass, foliage and root biomass; and stem mortality, mean annual increment and stand volume in *A. cordata*.

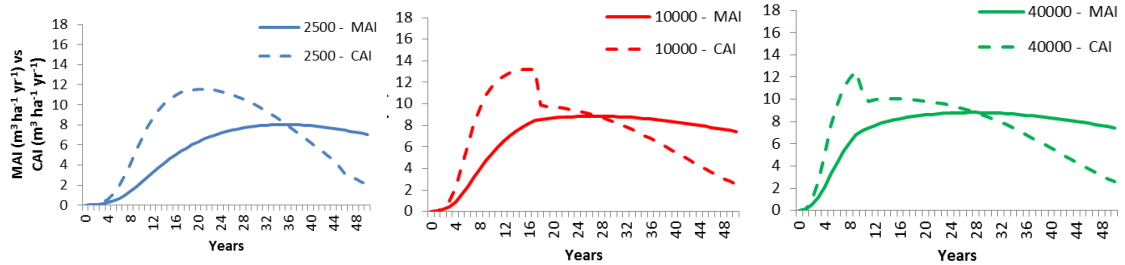

Figure 5-6: Mean annual volume increment (MAI) with mean current annual volume increment (CAI) for *A. cordata*.

5.3.3 *P. sitchensis*

Root and foliage biomass were projected to increase relatively quickly in *P. sitchensis* compared to *E. nitens* or *A. cordata.* The rate of root and foliage biomass accumulation was projected to decline from year 20 onwards. The projected AWB, root and foliage biomass accumulation at low planting density was predicted to occur relatively slowly than at the medium and high densities in *P. sitchensis*. However, stem biomass converged at year 20 at the three planting densities. Thereafter the growth rate of trees planted at the lowest planting density was predicted to increase above that of those planted at the other densities. Stem biomass accumulation had not levelled off by the end of the 50-year projection period for any planting density.

Mortality increased at the densest stocking from year 8 onwards (Figure 5-7), with the stocking levels predicted to be similar to the medium stocking by year 12. Thereafter, mortality was predicted to continue at a high rate at the densest stocking to the end of the 45-year projection period. At the end of that period there was <410 stems ha^{-1} difference between the low, medium and high planting densities, which were predicted to have 1,596, 2,006 and 1,795 stems ha^{-1} (36, 90 and 96% mortality, respectively). MAI was projected to increase at a similar rate for all spacings until year 10. The model projected a decline in MAI at the medium spacing to a value below that of trees grown at the low spacing. The MAI continued to increase to the end of the projection period at the higher planting density, but high mortality had reduced stocking levels by almost 95%. Trees planted at high density, with a predicted 5% of stems remaining at the end of the projection, produced the highest stand volume of the three planting densities.

The rotation length was estimated at 35, 38 and 42 for low, medium and high planting densities, respectively (Figure 5-8). The predictions indicate that root biomass, MAI and stand volume would vary between the planting densities with the values for the middle density being lower than those for the low or high densities. The AWB_{15} increased from 67 to 85 t ha^{-1} with as planting density increased from low to high density (Table 5-11).

Table 5-11: Model projections growth at three planting densities in *P. sitchensis*. Rotation length (RL) was defined as the point at which the MAI and CAI curves intersected (Figure 5-8). Biomass and volume production were estimated over this period. Biomass production over a standardised period of 15 years was also estimated.

Planting density	MAI_{RL} (m^3 ha^{-1} yr^{-1})	$Stocking_{RL}$ (ha^{-1})	RL	Basal $area_{RL}$ (m^2 ha^{-1})	AWB_{RL} (t ha^{-1})	Root $biomass_{RL}$ (t ha^{-1})	Stand $volume_{RL}$ (m^3 ha^{-1})	AWB_{15} (t ha^{-1})
2×2 m (2,500)	22.519	2,396	35	93.477	197.183	15.902	788.162	67.086
1×0.5 m (20,000)	20.180	2,141	38	102.056	188.330	13.980	766.823	80.829
0.5×0.5 m (40,000)	30.238	1,909	42	130.825	210.599	13.034	1,269.977	85.247

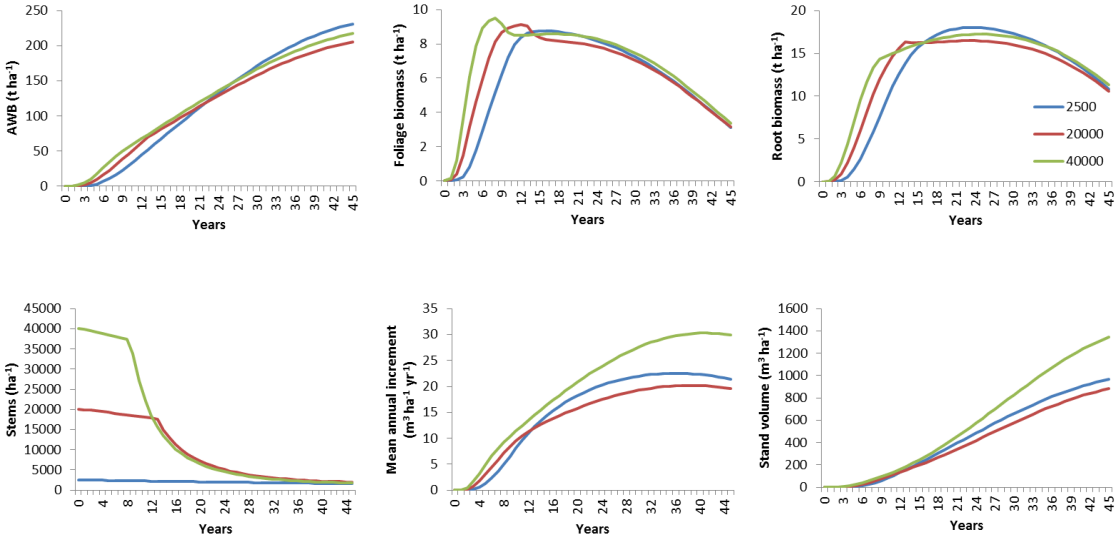

Figure 5-7: Model projections of stand development at three planting densities of above-ground woody biomass, foliage and root biomass; and stem mortality, mean annual increment and stand volume in *P. sitchensis*.

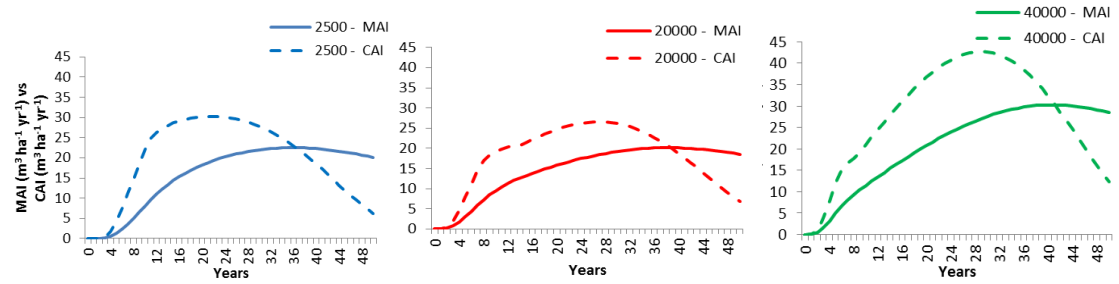

Figure 5-8: Mean annual volume increment (MAI) with mean current annual volume increment (CAI) for *P. sitchensis*.

5.3.4 Projected effects of stocking levels on stand growth

The model was used to predict growth at various stocking levels (i.e. not just the three stocking levels studied at Johnstown Castle) commencing at 1,600 stems ha^{-1} (Table 5-12). Productivity of *E. nitens* increased until stocking reached 4,444 stems ha^{-1} (1.5×1.5 m) at which point stand $volume_{15}$ and AWB_{15} declined. As stocking was increased, *A. cordata* was estimated to produce the lowest stand $volume_{15}$ and AWB_{15} of the three species. The AWB_{15} in *A. cordata* and *P. sitchensis* was estimated to increase until stocking reached 15,625 stems ha^{-1} (0.8×0.8 m) and 10,000 stems ha^{-1} (1×1 m), respectively, before declining. The rate of increase in *P. sitchensis* stand $volume_{15}$ and AWB_{15} was low as stocking was increased from 1,600 to 10,000 stems ha^{-1}. Stand volume and AWB_{15} of *E. nitens* was at least double that of *A. cordata* or *P. sitchensis* at all stocking levels.

Table 5-12: Estimation of stand volume and above-ground woody biomass production over a 15-year rotation length (AWB_{15}) with alternative planting densities for the three species. Red text indicates a predicted decrease in stand $volume_{15}$ and AWB_{15}.

Species	Spacing	Planting density	$Stocking_{15}$ (ha^{-1})	Stand $volume_{15}$ (m^3 ha^{-1})	AWB_{15} (t ha^{-1})	AWB_{15} Increase or decrease
E. nitens	2.5×2.5	1,600	1,508	524.722	139.944	
	2×2	2,500	2,357	600.500	146.236	↑
	1.8×1.8	3,086	2,909	635.835	148.440	↑
	1.6×1.6	3,906	3,627	669.379	149.645	↑
	1.5×1.5	4,444	3,784	659.083	146.517	↓
A. cordata	2.5×2.5	1,600	1,395	72.505	31.135	
	2×2	2,500	2,179	85.601	36.759	↑
	1.8×1.8	3,086	2,690	91.475	39.281	↑
	1.6×1.6	3,906	3,404	97.711	41.959	↑
	1.4×1.4	5,102	4,447	104.269	44.775	↑
	1.2×1.2	6,944	6,052	111.080	47.700	↑
	1×1	10,000	8,716	118.022	50.681	↑
	0.8×0.8	15,625	11,872	121.657	52.242	↑
	0.7×0.7	20,408	12,196	120.027	51.542	↓
P. sitchensis	2.5×2.5	1,600	1,394	164.810	82.822	
	2×2	2,500	2,179	166.786	83.815	↑
	1.8×1.8	3,086	2,690	167.650	84.249	↑
	1.6×1.6	3,906	3,404	168.565	84.709	↑
	1.4×1.4	5,102	4,447	169.537	85.197	↑
	1.2×1.2	6,944	6,052	170.576	85.720	↑
	1×1	10,000	8,715	171.698	86.284	↑
	0.8×0.8	15,625	13,619	132.816	66.744	↓

5.3.5 Impact of climate change on SRF productivity

The anticipated changes to Ireland's temperature and precipitation was predicted to have a positive effect on growth, with the exception of the highest density planting of *E. nitens* where stand volume was reduced (Table 5-13). The differences in above- and below-ground biomass estimates as climate changed from current to the two simulated scenarios were small but increased with stocking in all three species. Mortality rates did not increase at the low planting density for any species but declined for the medium and high planting densities as the climate changed from best- to worst-case scenarios.

Table 5-13: Impact of simulated climate changes, where temperature and precipitation were altered in line with best and worse-case scenarios (RCP2.6 and RCP8.5) on stocking, above and below-ground biomass allocation, stand volume and rotation length. A comparison was made between the AWB_{RL} estimated under the simulated climate and under current climate. The red text indicated a reduction in productivity as scenarios increase from current to worst case.

Planting density	RCP scenario	RL	Stocking (ha^{-1})	Stand volume ($m^3\ ha^{-1}$)	Root biomass ($t\ ha^{-1}$)	AWB_{RL} ($t\ ha^{-1}$)	Difference in AWB_{RL} ($t\ ha^{-1}$)
E. nitens							
2×2 m (2,500)	**Current**	**20**	**2,298**	**1,102.692**	**10.685**	**180.838**	
	2.6	20	2,298	1,107.672	10.721	181.712	+0.874
	8.5	20	2,298	1,112.429	10.761	182.547	+0.835
1×1 m (10,000)	**Current**	**11**	**9,107**	**1,031.273**	**9.215**	**94.441**	
	2.6	11	9,054	1,032.175	9.230	94.715	+0.274
	8.5	11	9,005	1,033.024	9.248	94.973	+0.258
0.5×0.5 m (40,000)	**Current**	**7**	**30,272**	**610.136**	**7.055**	**51.799**	
	2.6	7	30,090	609.745	7.067	51.956	+0.157
	8.5	7	29,922	609.383	7.082	52.101	+0.145
A. cordata							
2×2 m (2,500)	**Current**	**35**	**1784**	**280.791**	**13.113**	**117.099**	
	2.6	35	1784	283.288	13.201	118.140	+1.041
	8.5	35	1784	285.153	13.267	118.918	+0.778
1×1 m (10,000)	**Current**	**24**	**4110**	**211.691**	**14.522**	**88.787**	
	2.6	24	4063	212.899	14.592	89.294	+0.507
	8.5	24	4029	213.802	14.644	89.673	+0.379
0.5×0.5 m (40,000)	**Current**	**26**	**3539**	**228.722**	**14.655**	**95.689**	
	2.6	26	3499	229.988	14.725	96.218	+0.529
	8.5	26	3471	230.935	14.778	96.614	+0.396
P sitchensis							
2×2 m (2,500)	**Current**	**35**	**1,784**	**788.162**	**15.902**	**197.183**	
	2.6	35	1,784	793.611	15.997	198.352	+1.169
	8.5	35	1,784	797.800	16.070	199.250	+0.898
1×0.5 m (20,000)	**Current**	**39**	**2,388**	**766.823**	**13.980**	**188.330**	
	2.6	39	2,290	792.877	13.676	192.310	+3.98
	8.5	39	2,273	797.681	13.743	193.038	+0.728
0.5×0.5 m (40,000)	**Current**	**35**	**2,396**	**1,033.316**	**15.855**	**187.986**	
	2.6	35	2,375	1,041.564	15.937	188.811	+0.825
	8.5	35	2,360	1,047.943	16.000	189.447	+0.636

5.4 Discussion

Using data from the trial at Johnstown Castle combined with some information obtained from the literature, the study established a set of parameter values for use with 3-PG model for *E. nitens, A. cordata* and *P. sitchensis*. Stand development was projected for the three species in response to different planting densities. The projected output provided a good fit to the calibration data for all species.

5.4.1 Predicted yield and rotation length

The projected intersection of mean annual increment (MAI) and current annual increment (CAI) curves determined the rotation length (RL) and an estimation of the maximum stand productivity (Goundrey, 1960). The projected rotation length was different for each planting density and species in this study. Higher stand densities often delay the age that peak MAI is achieved (Schönau, 1982). However, in the three species studied, RL declined as planting density increased, and in most cases, the peak of MAI was not delayed. The MAI of a SRF species is required to peak at a young age if large quantities of biomass are to be produced within a short rotation period and to make the approach economically viable (Leslie et al., 2019). The selected rotation length of 15 years (RL_{15}) may not represent the optimal harvesting age for SRF. However, this enabled the comparison of the output of all spacings and species in the study. Only *E. nitens* was projected to have a rotation length close to RL_{15}, with *A. cordata* and *P. sitchensis* exceeding it with > 20 years at all planting densities.

The growth strategy of *E. nitens* involves allocating more biomass to above-ground than to below-ground components at all three planting densities evaluated in the polytunnel (Chapter 3). Projections indicate that the above-ground woody biomass (AWB) yield in *E. nitens* was greater than in *A. cordata* or *P. sitchensis* at all planting densities. When alternative planting densities to those used in the trial were modelled, the projected AWB was greatest at 3,900 stems ha^{-1} (c. 1.6×1.6 m spacing). The model indicated that the optimum planting density for *E. nitens* was much higher than the 1,800 to 2,000 stems ha^{-1} recommended by Thompson et al. (2012) or the 2,000 recommended in the Forestry for Fibre scheme (DAFM, 2018).

In this study, the RL for *E. nitens* was projected to be 11 and 20 years at the medium and low planting densities. The estimated RL of 11 – 20 years in this study is

longer on average than the 6 – 12 years suggested by González-García et al. (2015), which is likely due to the difference in climate between Ireland and Spain (Table 5-4). The model projected a RL of 11 years for the 10,000 stems ha^{-1} stocking, which results in a rotation that is shorter than the 15-year rotation selected for SRF. The greater productivity of this species at these planting densities would give *E. nitens* an advantage over the other species.

The projections of biomass yield at all planting densities were lower in *A. cordata* than in the other species. Although the AWB_{15} increased from 30 t ha^{-1} at low to 50 t ha^{-1} at medium planting density, the mortality rate also increased to nearly 50%. Thus, the economic loss due to tree mortality is likely to outweigh any advantage of planting at a higher density for this species. Information on RL was not available from the literature (to this author's knowledge) for comparison with *A. cordata* results here. However, data obtained for *A. incana* from over six countries in northern Europe showed that stocking rates of 2,460 to 14,000 stems ha^{-1} resulted in an MAI of 7 to 12 m^3 ha^{-1}, with a stand volume of 252 to 420 m^3 ha^{-1} at 35 years (Aosaar et al., 2012). Therefore, the projected MAI for *A. cordata* of ≈ 8 m^3 ha^{-1} at 35 years with a stand volume of 281 m^3 ha^{-1} for 2,500 stems ha^{-1} projected by 3-PG is realistic. Although the comparison is not for the same species it provides some confidence in the parameter values used for *A. cordata.* The results of this study bring into question the suitability of *A. cordata* as a SRF crop species in Ireland.

Projections showed that at full rotation, the stand volume increased as planting density increased in *P. sitchensis*. Similarly, when stand volume was projected for alternative planting densities to those used in the field trial, stand volume increased as planting density increased. However, the increase was very small in that species compared with *E. nitens* and *A. cordata.* The main parameter values, which were used in the model to predict outputs at other planting densities, originated from samples growing at 2×2 m spacing. Therefore, the parameter values may not take into account small changes in growth that may occur at these alternative planting densities (as shown in Table 5-5 for the three-field trial spacings). Based on the model projections for a 15-year rotation, the yield achieved at the 2.5×2.5 m spacing is the best option for *P. sitchensis* as higher planting density provides only a marginal increase in yield.

RL was predicted to range from 30 to 39 years in Ireland in *P. sitchensis*, based on standard planting density of 2,500 stems ha^{-1} (2×2 m) but will also depend on yield class (Lekwadi et al., 2012). The 3-PG model projected a RL of 35 and 38 years at planting densities of 2,500 and 10,000 stems ha^{-1}, respectively. This result confirms the rational of planting *P. sitchensis* at 2,500 stems ha^{-1} in conventional forestry systems in Ireland. A projected rotation length, which is in excess of 35 years at all stocking levels, demonstrates that this species is probably not suited to RL_{15} as it would involve harvesting before it achieved its greatest biomass production potential.

5.4.2 Future climate impact

The simulated changes of the future climate in Ireland did not adversely affect productivity at any of the planting densities. In fact, productivity increased in all cases. However, at the medium and high planting densities mortality increased as the climate change scenarios worsened. This may be due to the changes in temperatures and available soil water, increasing transpiration of the denser canopies. The simulations also indicated an increasing allocation to below-ground biomass, probably a response to low soil water availability. Research into the effects of climate change on *P. sitchensis* in Ireland indicated that soil water availability (water logging in the west and dry conditions in the south) could negatively impact growth (Berned and Nieuwenhuis, 2017). Overall these simulations suggest that forestry, and in particular SRF, will continue to be a sustainable land use in the short- to medium-term on suitable soil types.

5.4.3 Model limitations

Parameterising 3-PG sufficiently has proven difficult in many studies, as there is a requirement for data which are often not available (e.g. below-ground biomass) (Sands, 2004). Root data, litterfall rates and seedling biomass were estimated for the three species based on default values for *E. globulus,* as these data were not available from the Johnstown Castle study and other more appropriate data were not available from the literature. Litterfall rates are an important variable in the 3-PG model and are used in the calculation of carbon balance, foliage mass and leaf area index. Root data were used to parameterise and validate model partitioning to roots and within the water-balance sub-model (Sands and Landsberg, 2002).

The larger the calibration data set the greater the accuracy that can be achieved with the output of 3-PG or any other model. The use of Irish data sets, particularly those describing stem mass and leaf area index, would improve the calibration of the model and allow for more rigorous testing of parameter estimations.

5.5 Conclusions

The model projections allowed an assessment of the impact of initial spacing (and subsequent competition stress) on the productivity of the three species included in the Johnstown Castle trial. The study also allowed a consideration of the suitability of such species for management as short rotation crops. When the above-ground biomass at 15 years was compared, the predicted productivity was substantially higher in *E. nitens* than in *P. sitchensis* or *A. cordata* at all planting densities*. E. nitens* grows rapidly during the juvenile period of growth making it an ideal candidate for the production of large quantities of biomass over a short rotation. The results of the modelling exercise suggest that the RL of *E. nitens* could be reduced to 11 years with projected productivity of almost 125 t AWB ha^{-1} at 10,000 stems ha^{-1}. Based on model projections, *A. cordata* is not suitable for SRF, since it produced substantially smaller quantity of AWB than either *E. nitens* or *P. sitchensis*. The slow initial growth rate and projected optimal rotation length of c. 35 years of *P. sitchensis* to maximise biomass production makes it an unsuitable species for biomass production in any likely SRF rotation period. Simulations of future climate conditions were projected to have a positive effect on growth, and provide an opportunity for increased productivity, at least in the short term, especially if the predictions of moisture availability are accurate.

5.5.1 Recommendations for future work

The 3-PG model's predictive strength depends on the quality of data inputs. Many of the parameter values were available for *P. sitchensis* and *E. nitens.* However, few data are available for use in parameterisation and calibration of the model for *A. cordata*. The parameter values used in this study for the three species lay the foundations for future work to further refine and improve estimated growth data with 3-PG. Further research is required to fully validate the model using appropriate independent data, matched for geographic location, climatic and site conditions for the three species

used in this study. The collection of root data or litterfall rates is onerous and time consuming but for modelling the development of species, such data are invaluable. The parameterisation and comparison of different planting densities had not previously been modelled using the 3-PG model. In addition, *E. nitens* and *A. cordata* have not been used in process-based models in Ireland. The modelling of stand development over short rotations, and the assessment of long-term sustainability of SRF systems, would be greatly improved with more accurate and species-specific data. In particular, data that better describe leaf litterfall rates and root biomass allocation patterns and root turnover rates are needed.

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6 General discussion

Short rotation forestry aims to exploit species with fast juvenile growth rates to produce biomass with a high wood density, but competition for light and nutrients will reduce productivity. Therefore, to fully exploit and manage the production potential of any species in a short rotation, an understanding of competition effects on growth is needed. Few studies have characterised the effects of competition on the very early development and potential yield of trees grown in short rotation forestry systems in Ireland. The aim of this study was to identify how *E. nitens, A. cordata* and *P. sitchensis* respond to planting density and to consider an optimum strategy for field deployment and management (e.g. spacing that is likely to maximise yield) in SRF systems. The dynamics of growth and biomass yield of the three species over a 4-year period was evaluated in a field trial and polytunnel experiment, with the aim of identifying competition at an early stage. The data, combined with information from the literature, were used in a model to predict growth, yield and rotation length at various planting densities.

6.1 Planting density effects

As expected, the growth and biomass characteristics differed with planting density and species, but the impact was more pronounced in the polytunnel experiment than in the field trial (Table 6-1). From early in its deployment *E. nitens* shed lower branches which resulted in a shallow but highly productive crown. The height to branch ratio increased, while the crown depth decreased, as planting density increased. Although the amount of biomass allocated to the branch and leaves declined, the proportion of biomass allocated to the stem increased as planting density increased. The allocation of more biomass to stems is a useful characteristic for SRF where biomass yield is the main objective. Despite shedding lower, less productive leaves and branches, *E. nitens* produced the largest quantity of biomass of the three species.

Higher planting densities resulted in a higher proportion of leaves in shade. As shade leaves respond to the lower light levels, photosynthesis rates decline (Loach, 1967). The competition for light results in stress in *E. nitens,* which is reflected in a

decline in chlorophyll concentration (Ch_{leaf}) prior to the shedding of the leaves and branches (Carter and Knapp, 2001). Although the Ch_{leaf} declined as planting densities increased, which implies that the leaves were under stress, photosynthesis rates remained similar across planting densities. This suggests that shade leaves are shed before lower light levels can result in a reduction in photosynthesis rates in *E. nitens*. This is an efficient growth strategy since it ensures that little biomass remains allocated to lower and less productive components.

Characteristics such as height, stem diameter, crown depth, branch length and crown volume were highly variable in *E. nitens* in the field, but the degree of variation was lower in the polytunnel. This may have been due to greater variability in nutrient and soil water availability in the field trial, which appeared to affect *E. nitens* more than *A. cordata* or *P. sitchensis*. In addition, climatic conditions varied greatly at the site (which included seasonal episodes of drought, other periods when conditions were very wet, freezing winter temperatures and high winds). In contrast, climatic conditions in the polytunnel were relatively constant. A high degree of variability in growth rates, attributed mostly to variations in soil type and nutrient availability, has been observed in eucalyptus species in Brazil (Campoe et al., 2012). The high variability in a stand of *E. nitens* in Tasmania was attributed to genetic factors (Neilsen and Gerrand, 1999). The same provenance of *E. nitens* was used to produce the seedlings used for both the polytunnel and field trial in this study. Variation in growth was much higher in the field than in the polytunnel, suggesting that environmental rather than genetic factors caused this variation in the field.

The trees of *A. cordata* were tall with wide crowns but had small-diameter stems. Tree height and branch length decreased as planting density increased in the polytunnel in *A. cordata*, whereas height increased, and branch length was unaffected by planting density in the field trial. Photosynthesis rates declined in shade leaves as planting density increased in *A. cordata* in this study. Similarly, net photosynthesis declined in the lower canopy as planting density increased in *A. rubra* in Scotland (Proe et al., 2002). Ch_{leaf} and photosynthesis rates were higher in the shade leaves of *A. cordata* in the field than in the polytunnel. These results indicate that the 4-year-old plants in the field were acclimating better to shade levels than those in the polytunnel. Nevertheless, biomass production was very low in the field, but was considerably

higher in the polytunnel. Differences in yield were also apparent, with above-ground biomass decreasing as planting density increased in the polytunnel. However, planting density had no significant effect on above-ground biomass in the field trial. This implies that competition had little impact in the field, even at the highest density of 40,000 stems ha^{-1}. *A. cordata* produced the highest quantity of biomass of the three species in the polytunnel. In contrast, biomass yields of *A. cordata* were similar to *P. sitchensis* and lower than *E. nitens* in the field trial. These results indicate that *A. cordata* may be the most sensitive of the three species to environmental conditions. It is likely that the warm, moist conditions of the polytunnel favoured growth, whereas the cooler and more variable field conditions greatly reduced growth rates. Wind exposure in the field may have magnified these effects perhaps leading to drought stress, even during periods of high-water availability (i.e. causing physiological drought). *A. cordata* grew rapidly in the polytunnel, demonstrating that it can grow vigorously if conditions are suitable, producing a large quantity of biomass, at least in a shorter growth period. The ability of *A. cordata* to grow rapidly in a short period indicates it may be more suitable to a coppice than a SRF system, where rapid early (1-2 years) growth is likely to produce sufficient yield. In a study of *A. rubra* in Scotland, close spacing reduced individual tree size, but increased biomass per unit area and fully occupied the site 2 years after planting, but productivity had already begun to decline 5 years after planting (Proe et al., 2002). The branches of competing trees overlap greatly in *A. cordata,* unlike that observed in the other species, suggesting that it may also be a good choice for mixed species plantations.

P. sitchensis grew more slowly than the other two species and accumulated more branches per unit stem height, resulting in a highly dense tree crown. Spacing effects resulted in the formation of a dense canopy in *P. sitchensis* after 14 years growth in Scotland (Ford and Deans, 1978). Above-ground growth rates were relatively slow in the polytunnel and field trial in comparison to *E. nitens* or *A. cordata*. Higher planting densities reduced stem diameter, stem volume, branch length, crown volume, Ch_{leaf}, leaf dry weight and leaf area in *P. sitchensis* in the polytunnel. In contrast, none of these characteristics were affected in the field trial. Specific leaf area was the only characteristic that indicated an effect of planting density in the field. This suggests that, although above-ground biomass accumulation was slower than in either

of the other two species, *P. sitchensis* was responding to competition at the high planting density. The relatively small SLA in this species during its early growth period limits photosynthate production (Cannell, 1987). This decrease in SLA due to higher stocking may also result in a reduction in photosynthate production, suggesting that a high planting density (>10,000 stems ha^{-1}) would decrease potential productivity in *P. sitchensis* under a SRF system and the modelled projections of the field trial growth support this interpretation, as discussed below.

6.2 Growth projections

Since data were available only for the four-year period of initial growth in this study, a model was used to project development over the full period of a likely SRF rotation. Modelling was used to estimate the impact on yield of variations in planting densities over a 15-year rotation. The data from the Johnstown Castle trial demonstrated that *E. nitens* allocated the greatest quantity of biomass to above-ground components during the very early stages of development. The predictions indicated that this trend would continue for >20 years. The predicted rotation length was substantially shorter for *E. nitens* than for *A. cordata* or *P. sitchensis* and the estimated stand volume and biomass yield were greater, regardless of planting density. The model predicted that a stocking of c. 3,900 stems ha^{-1} (c. 1.5×1.5 m) would maximise biomass yield in *E. nitens*, producing an estimated above-ground biomass of 150 t ha^{-1} (670 m^3 ha^{-1}) at 15 years before production would plateau and start to decline. The currently recommended planting density for *E. nitens* is 1,800 - 2,000 stems ha^{-1}, but was based on scant data (Thompson et al., 2012). The results of this study indicate that a higher density would be preferable to maximise production over a shorter rotation period.

At the higher stocking densities all estimations of biomass yield in *A. cordata* were lower than for *E. nitens* or *P. sitchensis.* Assuming a standardised 15-year SRF rotation and establishing 2,500 stems ha^{-1} (2×2 m), an estimated biomass yield of 38 t ha^{-1} was predicted. The model estimated that a stocking density of up to 15,600 stems ha^{-1} could be used before a reduction in total biomass would occur, which seems unrealistic. However, *A. cordata* grew tall and thin in response to the highest planting density used in this study, with considerable live-branch overlap, suggesting that the species can be grown at high densities without greatly increasing mortality. A

rotation of >24 years was predicted for *A. cordata* to maximise its biomass potential. This rotation is likely to be too long for an SRF system and the predicted biomass yield is relatively low compared to that predicted for *E. nitens* or *P. sitchensis*

The 3-PG model predicted that *P. sitchensis* could produce 70 t ha^{-1} (above-ground biomass) over a 15-year rotation, assuming an initial stocking of 1,600 stems ha^{-1} (2.5×2.5 m). Further increases in stocking were estimated to result in only a small increase in biomass yield. This is likely to have been caused by model parameterisation values not reflecting the changes in growth which occur as planting density increases. It may also reflect that default values were used for predicting mortality, and these may not accurately reflect the rate of stand mortality. It can be anticipated that highly competitive circumstances (high planting densities) would increase mortality rates and result in more growing space per tree and higher growth rates. This implies that planting densities in excess of 1,600 stems ha^{-1} would not increase biomass yield in *P. sitchensis.* Although *P. sitchensis* grew slowly in the field trial, it produced a higher biomass yield than *A. cordata*. The model also predicted a higher biomass yield for *P. sitchensis* than *A. cordata* over a 15-year rotation. Its characteristic slow growth during the establishment phase makes it unsuitable for use in SRF systems. A rotation length of 30+ years is needed to maximise its biomass potential. *P. sitchensis* is the most frequently planted forestry species in Ireland (Forest Service, 2013). It accounts for over 50% of the total forest estate. Therefore, one potential advantage of using *P. sitchensis* in SRF is that it could be regarded as a "safe" species, i.e. a stand that has been planted for SRF could be readily converted to a conventional forestry plantation if economic or other conditions dictated. However, the results from the study clearly show that this species would not be suitable for biomass production at rotations of less than 35 years

Despite the limited amount of data available to develop the model used in this study (as discussed below), the results showed a reasonable correlation with the growth data obtained from the field trial. In particular, few data were available for *A. cordata,* so data for other species had to be substituted, weakening the model predictions for this species. The estimated output for *A. cordata* should therefore be interpreted with caution.

Table 6-1 Morphological and physiological characteristics and their effectiveness in detecting competition in the polytunnel experiment and field trial. The letters indicate which treatments differed significantly between low (L), medium (M) and high (H) planting densities; (**) = indicates where all treatments were significantly different; no competition effects = (N); and measurement not taken = (-). Some leaf measurements were made at different crown positions (sun or shade leaf).

Growth characteristics	*E. nitens*		*A. cordata*		*P. sitchensis*	
	Polytunnel	Field	Polytunnel	Field	Polytunnel	Field
Tree height (m)	L/H	N	M/H	L/H	N	N
Root collar diameter (mm)	**	N	**	L/H	**	N
Branch length (cm)	**	N	**	N	**	N
Branch diameter (mm)	-	N	-	L/H	-	N
Stem volume (m^3)	L/M	L/H	**	N	M/H	N
Height: branch ratio	**	**	L/M	M/H	L/M	N
Crown depth % of height	-	L/H	-	N	-	N
Crown volume (m^3)	L/M	N	L/M	N	L/M	N
Leaf area (cm^2)	L/H(shade)	N	**	N	L/M(sun)	N
Leaf DW (g)	L/M(shade)	N	**	N	L/M(sun)	N
Specific leaf area ($cm^2\ g^{-1}$)	N	N	M/H	N	N	L/M
Leaf area index	L/M	N	M/H	**	N	M/H
Chlorophyll concentration ($mg^{-1}\ m^2$)	**(shade)	M/H	L/H(shade)	N	N	N
Rate of photosynthesis (µmol (CO_2) $m^{-2}\ s^{-1}$)	L/H(shade)	N	L/H(shade)	M/H	-	-
Transpiration rate (mmol H_2O $m^{-2}\ s^{-1}$)	L/H(shade)	N	N	M/H	-	-
Stem biomass (g)	L/M	N	**	N	**	N
Branch biomass (g)	L/M	N	L/M	L/H	**	N
Above-ground biomass (g)	L/M	N	**	N	**	N
Below-ground biomass (g)	L/M	-	L/H	-	**	N
Root: shoot ratio	L/H	-	N	-	M/H	-

7 Conclusions

The growth response to planting density differed between species. *E. nitens* has a relatively fast rate of growth compared to the other two species and develops a highly efficient and productive crown. This resulted in the greatest stand biomass of the three species. The results indicated that a higher stocking level than is currently used in practice is likely to increase biomass yield in *E. nitens.* If a 15-year rotation length was selected, the growth model indicated that planting density should be increased to 3,900 – 4,500 stems ha^{-1} (1.6×1.6 – 1.5×1.5 m) from the currently recommended 2,500 stems ha^{-1} (2×2 m). However, the model also indicated that a slightly shorter rotation (11 years) could be advanced using a higher planting density than 3,900 stems ha^{-1}. *A. cordata* grew tall and thin trees as planting density increased. This species spread its branches into the crowns of neighbouring trees, demonstrating that it tolerated competition very well. However, *A. cordata* was the least productive species, with the lowest predicted biomass yield, suggesting it is unlikely to be a suitable SRF species in

Ireland at least in the current climate. In general, planting density had no significant effect on the growth in *P. sitchensis* during the first four years of field growth, but competition was identified in leaf-level responses. This indicates that although there were very slight changes in growth characteristics resulting from planting density in *P. sitchensis,* competition effects were beginning to manifest. The slow initial growth rate would limit biomass accumulation over a short rotation. This development strategy makes is unsuitable for use in a short rotation system.

8 Limitations of study and suggestions for future research

This study was limited to three species with varying potential for use in a short rotation forestry system in Ireland. However, other species on the DAFM-recommended list, or other tree species not on this list, might be suitable candidates for SRF so should also be assessed in a similar way to determine their suitability for use in SRF in Ireland. The growth data obtained for *A. cordata* in this study provides some initial information, but further investigations over a longer period of time are needed to determine if the species has potential as a SRF species in Ireland. Root biomass data were not determined at the time of harvesting in the field trial, yet such data are needed to better assess biomass allocation patterns in each species and to improve model predictions. Photosynthesis rates in *P. sitchensis* were not assessed in this study, which limited the ability to characterise growth during the early stages (first 4 years) of growth. Photosynthesis rates and chlorophyll concentration changed with planting density, but the measurements were made at irregular intervals. Therefore, more measurements carried out more frequently and over a longer period of time are needed to improve our knowledge on the effects of planting density on these species and in improving the model predictions. The data in this study were obtained from one site in Co. Wexford, augmented by data from a polytunnel experiment, so data from more sites would provide more accurate and robust information for SRF in Ireland. The 3-PG model projections developed in this study over-relied on the use of default values. In particular, there was not enough information for some variables, i.e. leaf litter-fall rate, seedling biomass data (allocation between stem, foliage and roots), LAI or stem volume change over any extended period of time, all of which reduced the accuracy of the model. Short trials (i.e. one year) could be used to assess litter-fall

rates. The model was calibrated using a small quantity of data from many different data-sets and could be improved by using more extensive data-sets over longer growth-periods.

8.1 References

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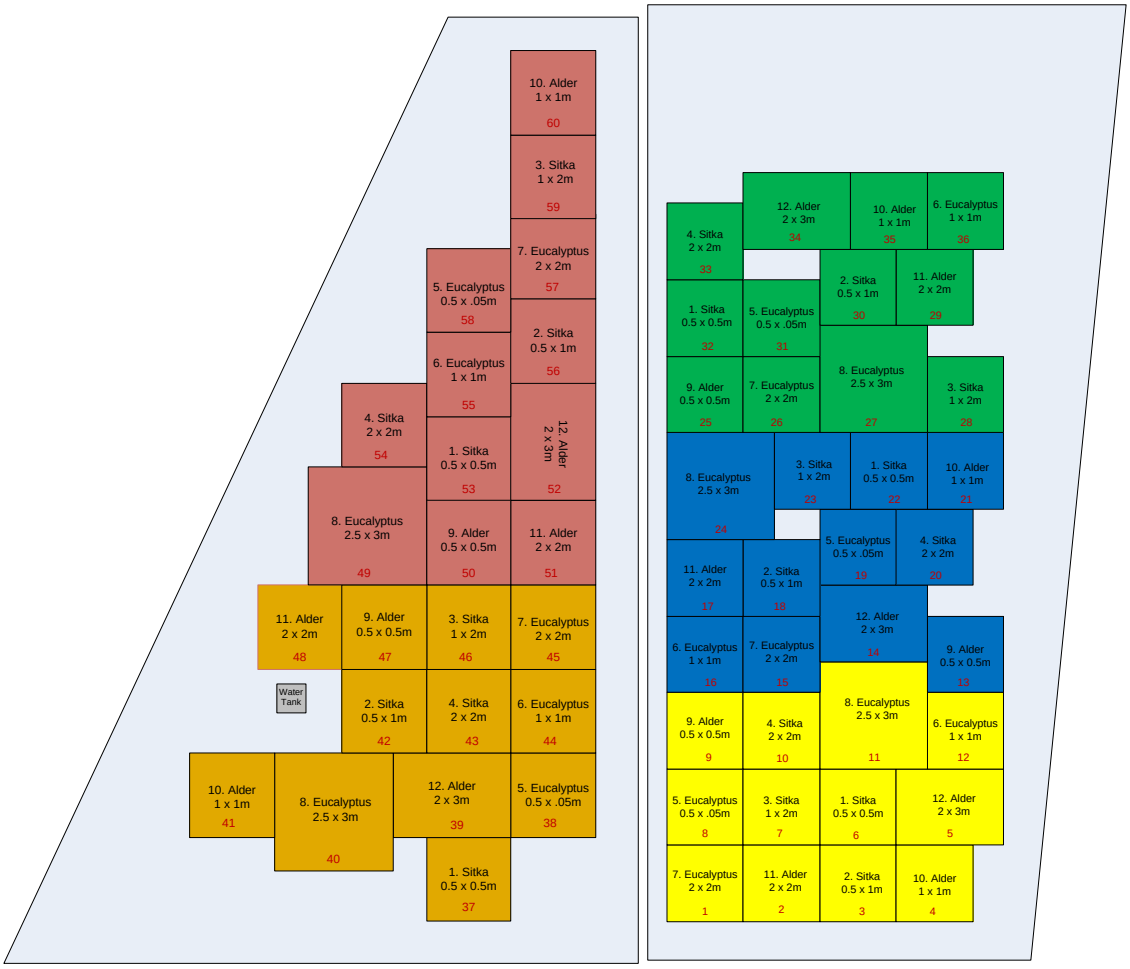
Appendix A

Table A-1: Experimental design of potted experiment at Teagasc, Kinsealy Research Station, Dublin with the three species used in the experiment, *E. nitens* (EN), *A. cordata* (AC) and *P. sitchensis* (PS).

	Number	Block/ Row 1	Density		Number	Block/ Row 2	Density		Number	Block/ Row 3	Density
Buffer	30	AC	4	Buffer	31	AC	8	Buffer	90	AC	1
Unit 21	29	AC	8	Unit 22	32	AC	4	Unit 25	89	AC	1
	28	AC	4		33	AC	1		88	AC	8
	27	AC	1		34	AC	8		87	AC	4
Unit 20	26	AC	4	Unit 23	35	AC	8	Unit 26	86	AC	4
	25	AC	8		36	AC	1		85	AC	8
	24	AC	1		37	AC	4		84	AC	1
Unit 19	23	AC	1	Unit 24	38	AC	4	Unit 27	83	AC	4
	22	AC	8		39	AC	1		82	AC	8
	21	AC	4		40	AC	8		81	AC	1
Buffer	20	EN	8	Buffer	41	EN	1	Buffer	80	EN	8
Unit 12	19	EN	1	Unit 13	42	EN	4	Unit 18	79	EN	8
	18	EN	8		43	EN	8		78	EN	1
	17	EN	4		44	EN	1		77	EN	4
Unit 11	16	EN	8	Unit 14	45	EN	1	Unit 17	76	EN	8
	15	EN	4		46	EN	8		75	EN	4
	14	EN	1		47	EN	4		74	EN	1
Unit 10	13	EN	8	Unit 15	48	EN	8	Unit 16	73	EN	1
	12	EN	4		49	EN	4		72	EN	8
	11	EN	1		50	EN	1		71	EN	4
Buffer	10	PS	4	Buffer	51	PS	1	Buffer	70	PS	8
Unit 3	9	PS	8	Unit 4	52	PS	8	Unit 9	69	PS	4
	8	PS	4		53	PS	4		68	PS	8
	7	PS	1		54	PS	1		67	PS	1
Unit 2	6	PS	1	Unit 5	55	PS	8	Unit 8	66	PS	8
	5	PS	8		56	PS	4		65	PS	4
	4	PS	4		57	PS	1		64	PS	1
Unit 1	3	PS	4	Unit 6	58	PS	4	Unit 7	63	PS	8
	2	PS	1		59	PS	8		62	PS	1
	1	PS	8		60	PS	1		61	PS	4
Buffer	-	PS	4	Buffer	-	PS	4	Buffer	-	PS	4

Appendix B



B 1: Field trial layout at the Johnstown Castle site in Co. Wexford. The trial was laid out with 60 plots, in five blocks, with four planting densities per species per block. The three species were *E. nitens* (Eucalyptus), *A. cordata* (Alder) and *P. sitchensis* (Sitka).